

TESIS DOCTORAL

AÑO 2018

HAPTIC PERCEPTUAL GROUPING: BEHAVIORAL AND NEUROPHYSIOLOGICAL CORRELATES

[AGRUPAMIENTO PERCEPTIVO HÁPTICO: CORRELATOS CONDUCTUALES Y NEUROFISIOLÓGICOS]

Antonio Prieto Lara Licenciado en Psicología

PROGRAMA DE DOCTORADO EN PSICOLOGÍA DE LA SALUD

Directora: Soledad Ballesteros Jiménez

Codirectora: Julia Mayas Arellano

Departamento de Psicología Básica II Facultad de Psicología UNIVERSIDAD NACIONAL DE EDUCACIÓN A DISTANCIA

HAPTIC PERCEPTUAL GROUPING: BEHAVIORAL AND NEUROPHYSIOLOGICAL CORRELATES

Autor:

Antonio Prieto Lara

Licenciado en Psicología

Directora de la Tesis:

Dra. Soledad Ballesteros Jiménez

Codirectora de la Tesis:

Dra. Julia Mayas Arellano

"Study hard what interest you the most in the most undisciplined, irreverent and original manner possible".

Richard Feynmann

Letter to J.M. Szabados (November 30, 1965)

Haptic Perceptual Grouping: Behavioral and Neurophysiological Correlates
Dedicado a ti "Abuelín",
porque todo lo bueno y recto que hay en mí es tu legado.

ACKNOWLEDGMENTS (AGRADECIMIENTOS)

Mientras escribo estas líneas, las últimas de una tesis doctoral que comencé hace ya casi cuatro años, mi mente hace un esfuerzo por recordar a todas aquellas personas y todos aquellos momentos que, de una u otra manera, han formado parte y han hecho posible este proyecto. Una tesis es una historia y, como todas las historias, será mejor contarla desde el principio.

El principio, como no podría ser de otra manera, se encuentra en la creación del Universo, pero no en el evento cósmico ocurrido hace más de 15.000 millones de años, si no en el libro de George Gamow que mis padres pusieron en mis manos (casi por casualidad) cuando aún no había cumplido los 8 años de edad. Por supuesto, en aquel momento no entendí prácticamente nada de lo que encerraban aquellas insulsas tapas rojas, pero su lectura comenzó a orientar hacia fines concretos un impulso que había sentido desde que podía recordar: una adictiva e insaciable curiosidad unida a una innata tendencia (en ocasiones exasperante) al escepticismo. Fueron mis padres quienes alimentaron ese impulso y lo apoyaron incondicionalmente hasta convertirlo en lo que hoy soy. "Gracias" es una palabra muy pequeña para expresar todo lo que les debo. Esta Tesis es tan suya como mía.

Gracias también a toda mi familia, porque ellos han sido y son mi refugio y mi ancla. Ellos me han dado la verdadera felicidad de vivir a su lado, de tenerlos cerca cuando más los he necesitado, de apoyarme incluso en los peores momentos y de confiar incondicionalmente en mí. A mi hermana, mis primos, tíos, abuelos, a todos, gracias por llevarme hasta aquí.

La UNED ha sido una parte importante de mi vida. Me acogió en su comunidad cuando lo necesité y me dio las herramientas para desarrollarme como estudiante

y científico. Aquí he conocido a gran parte de las personas que han marcado mi carrera investigadora. Nunca estaré lo suficientemente agradecido al profesor Marcos Ruiz, gracias a quien descubrí mi vocación dentro de la Psicología. Tampoco dejaré de admirar su rigor científico y su prodigiosa capacidad de análisis. Su ejemplo me guiará siempre.

Pedro, tú orientaste mi carrera durante mis (todavía) primeros pasos (esos años de Prácticum y Master) en la investigación. He aprendido a ser científico a tu lado y te considero mi Mentor y mi Amigo. Mi gratitud hacia ti es tan solo comparable a mi admiración. Nada de esto hubiese sido posible sin tu ayuda.

¡Sita Cris! Seis años ya desde que nos encontramos por primera vez en esta nuestra Facultad. Seis años siendo mi compañera, secuaz y Amiga, compartiendo grandes momentos a tu lado. Siempre has sido alguien muy especial para mí y espero que lo sigas siendo hasta el fin de los tiempos (o hasta que la Estrella de la Muerte destruya nuestro planeta, lo que llegue antes). Gracias y mil veces gracias.

Un apartado especial merecen mi Directora y Codirectora de Tesis. Solo puedo expresar mi agradecimiento a la Profesora Soledad Ballesteros por confiar en mí, por su guía durante todos estos años, por su apoyo y su consejo. El reto de trabajar a su lado ha sacado lo mejor que llevo dentro.

Julia, gracias por ser la mejor Codirectora que uno puede desear. Has compartido conmigo el día a día de todos estos años, me has enseñado y aconsejado más y mejor de lo que nunca hubiera podido imaginar. Me has ayudado tanto y en tantas ocasiones que no puedo ni alcanzar a recordarlas todas. Hemos trabajado codo con codo en una enorme cantidad de proyectos. Nunca olvidaré la

experiencia de trabajar a tu lado y espero que sigamos haciéndolo muchos años más.

No puedo olvidarme de mis compañeros del grupo de investigación y de laboratorio durante todo este tiempo. El profesor José Manuel Reales, con quien he compartido algunas de las charlas más interesantes sobre ciencia. La profesora Pilar Jiménez y el profesor Antonio Crespo. Mis compañeras Pilar Toril, Carmen Pita y Jennifer Riecker, que me han aguantado en el laboratorio y han compartido conmigo largas horas de trabajo. Y, por supuesto, de todos los integrantes de los Departamentos de Psicología Básica I y II donde he desarrollado mi actividad durante los últimos 6 años. A todos ellos ¡Gracias!

Tampoco me olvido de ti Vane, mi *partner in crime*. Cuantas horas de investigación y risas entre cafés, cervezas y pantallas de ordenador. Gracias por hacer de la Facultad y de nuestro trabajo algo mucho mejor.

Thanks to Professor Ivry, Hyosub, Ludovica, Darius and all the people in the CognAc lab. at the University of California Berkeley. You guys made my stay in CAL a wonderful experience and one of the most fruitful research and learning periods of my career. Of course, my table tennis skills also improved a lot (thanks to Darius and Hyosub, two impressive players).

Y, por supuesto, gracias a ti Lau. Mi pareja, mi compañera, mi amiga, quien durante los últimos casi 5 años ha reído y llorado conmigo, la que ha sufrido esta Tesis como ninguna otra persona, la que ha permanecido a mi lado en los buenos y en los malos momentos. A ti, que te basta una mirada para ver lo más profundo de

mí. Juntos hemos logrado esto y mil cosas más. Sea lo que sea lo que nos depare el futuro recuerda una sola cosa: ¡Te quiero!

INDEX

Acknowledgments	9
Symbol list	19
Abbreviation list	21
Acronyms list	23
Figure list	25
Table list	29
CHAPTER 1: Perceptual organization	31
1. The problem of organizing the world	33
2. Four different approaches to perceptual organization	34
2.1. The Gestalt psychology (structural simplicity)	35
2.2. The ecological point of view	36
2.3.Computational models	37
2.4.Neural approaches	38
CHAPTER 2: Perceptual Grouping	39
1. The grouping processes	41
2. The grouping principles	41
2.1.Classical grouping principles	42
2.2.New grouping principles	44
3. Methodological approaches to the study of perceptual grouping	46
3.1.Phenomenological (subjective)methods	47
3.2.Psychophysical (objective)methods	48
4. The laws of grouping: how do grouping principlesinteract?	51
4.1.Grouping quantification strategies	52
4.1.1.The trade-off strategy	52
4.1.2.The proximity-first strategy	54
5. Neural mechanisms of perceptual grouping	55
5.1.Neural correlates of grouping principles	56

	5.2. Neural correlates of other organizational phenomena	.57
Cl	HAPTER 3: Perceptual organization in the sense of touch	59
1.	Introduction	.61
2.	Anatomical and physiological bases of active touch (the haptic system)	.62
	2.1.Mechanoreceptors and their physiological mechanisms	.63
	2.1.1.Mechanoreceptors of the joints and muscles	.64
	2.1.2.Mechanoreceptors of the skin	.65
	2.2.The "what" and "where" systems in touch	.67
	2.3.Neural basis of touch	.71
	2.3.1.Anatomical basis	.71
	2.3.2.Neural basis of form and texture perception	.73
3.	Perceptual organization and grouping in the sense of touch	.75
	3.1.Figure/ground segregation	.76
	3.2. Grouping principles	.77
Cl	HAPTER 4: Objectives and hypotheses	81
1.	Objectives	.83
2.	Hypotheses	.84
Cl	HAPTER 5: Time Course of Grouping by Proximity and Similarity in a	
На	aptic Speeded Orientation Task	.87
	Introduction	
2.	Method	
	2.1. Participants	
	2.2. Stimuli and apparatus	
	2.3. Design and procedure	
2		
	Results	
4.	Discussion	.99
Cl	HAPTER 6: Alpha and beta band correlates of haptic perceptual groupin	ıg:
re	sults from an orientation detection task1	.03
	Introduction1	
	Method	

	2.1. Participants	115
	2.2. Apparatus and stimuli	115
	2.3. Procedure	117
	2.4. EEG pre-processing and epoch rejection	120
3.	Data analysis	122
	3.1. Analysis of behavioral data	122
	3.2. Independent Component Analysis (ICA) and component clustering	122
	3.3. Time frequency analysis and event-related spectral perturbations	125
	3.4. Statistical analysis	126
4.	Results	127
	4.1. Behavioral results	127
	4.1.1. Response times (RTs)	127
	4.1.2. Accuracy	128
	4.2. EEG dynamics	128
	4.2.1. IC-cluster Event-related Spectral Perturbations (ERSP) and por	wer
	spectra	131
5.	Discussion	134
	5.1. Faster responses to stimuli grouped by spatial proximity	135
	5.2. Event-related spectral changes associated with different grouping	
	conditions	137
	5.2.1. Left sensorimotor IC-cluster	137
	5.2.2. Right sensorimotor IC-cluster	138
	5.2.3. Left parietal IC-cluster	140
	5.2.4. Right parietal IC-cluster	141
	5.2.5. Occipital IC-cluster	143
	5.3. Shortcomings, limitations and future directions	145
6.	Conclusions	146
CI	HAPTER 7: Interactions dynamics between grouping principles in to	ouch:
ph	enomenological and psychophysical evidence	149
_	Introduction	
2.	Experiment 1. Perceived phenomenological strength	159
	2.1. Method	

	2.1.1. Participants	160
	2.1.2. Apparatus	160
	2.1.3. Stimuli	161
	2.1.4. Design and procedure	163
	2.2. Results	165
	2.2.1. Data for no-grouping condition (baseline)	166
	2.2.2. Data corresponding to the four grouping conditions	167
	2.2.3. Individual consistency	169
	2.2.4. Compatibility with and additive model of grouping effects	171
3.	Experiment 2	173
	3.1. Method	174
	3.1.1. Participants	174
	3.1.2. Apparatus and stimuli	175
	3.1.3. Design and procedure	175
	3.2. Results	176
	3.2.1. Response times and error rates	176
	3.2.2. Dominance dynamics and compatibility with additive effects	178
4.	General discussion	181
5.	Limitations and future directions	185
6.	Acknowledgments	187
CF	HAPTER 8: Behavioral and electrophysiological correlates of intera	ctions
be	tween grouping principles in touch: Evidence from psychophysical	
ine	direct tasks	189
1.	Introduction	195
2.	Experiment 1	200
	2.1. Method	200
	2.1.1. Participants	200
	2.1.2. Apparatus and stimuli	201
	2.1.3. Design and procedure	203
	2.1.4. EEG acquisition and pre-processing	205
	2.2. Data analysis	206
	2.2.1. Behavioral data	20 <i>6</i>

	2.2.2. Independent Component Analysis (ICA) and component	
	clustering	207
	2.2.3. Time/frequency analysis of event-related spectral perturbation	ıs
	(ERSP)	209
	2.3. Results	210
	2.3.1. Behavioral results	210
	2.3.2. EEG results: IC-cluster event-related spectral perturbations	212
3.	Experiment 2	218
	3.1. Method	219
	3.1.1. Participants	219
	3.1.2. Apparatus and stimuli	219
	3.1.3. Design and procedure	220
	3.1.4. EEG acquisition and pre-processing	221
	3.2. Data analysis	221
	3.2.1. Behavioral data	221
	3.2.2. Independent Component Analysis (ICA) and component	
	clustering	222
	3.2.3. Time frequency analysis of Event-related Spectral Perturbation	ıS
	(ERSP)	222
	3.3. Results	222
	3.3.1. Behavioral results	222
	3.3.2. Compatibility with an additive model of grouping effects	223
	3.3.3. EEG results: IC-cluster event-related spectral perturbations	225
4.	General discussion	230
	4.1. Dominance dynamics and additive effects of interactions between gro	ouping
	principles in touch	231
	4.2. Independent Component Analysis (ICA) and Event-related spectral	
	perturbation (ERSP)	233
	4.2.1. Left and right sensorimotor clusters	234
	4.2.2. Right parietal and pre-frontal clusters	236
	4.2.3. Left occipital cluster	237
5.	Shortcomings, limitations and future directions	239
6.	Acknowledgments	241

CHAPTER 9: General conclusions	243
CHAPTER 10: Agrupamiento Perceptivo en el Tacto; Correl	atos
Conductuales y Neurofisiológicos	253
References	263
Appendix I	297
Appendix II	299
Appendix III	303
Appendix IV	305

SYMBOL LIST

- **%:** Percentage
- **÷:** Grouping principles conjoined in competition.
- **μ:** Mu sensorimotor rhythm.
- **d:** Effect size.
- **D:** Normalized effect size.
- **F:** Fisher's F.
- **I:** Conjoined condition RT single condition RT.
- **n:** Sample size.
- $\eta^2 \mathbf{p}$: Partial eta squared.
- **p:** Probability (of the null hypothesis).
- R: Mean transformed rating.
- **r:** Pearson correlation coefficient.
- S²: Variance.
- t: Student's t.
- **u**: Source matrix.
- **W:** Unmixing matrix.
- x: Scalp EEG matrix.
- Z: Wilcoxon's Z.
- **α:** Alpha band.
- **β:** Beta band.
- **0:** Arcsine (angular) transformation.
- **O:** Grouping principles conjoined in cooperation.
- **Ω:** Ohm.

ABBREVIATION LIST

Ag: Silver.
Cl: Chlorine.
cm: Centimeter.
Comp.: Competitive.
Coop.: Cooperative.
dB: Decibel.
e.g.: Exempli gratia.
Exp.: Experiment.
Fac.: Facilitation.
Fig.: Figure.
Hz: Hertz.
i.e.: Id est.
Inc.: Incorporated.
Interf.: Interference.
Log: Logarithm.
Max: Maximum.
Min: Minimum.
min: Minute.
mm: Millimeter.
MonHap: Haptic Monitor
p: Proximity.
s: Similarity.

ACRONYMS LIST

ANOVA: Analysis of variance.

BEM: Boundary element head model.

EEG: Electroencephalography.

EMG: Electromyography.

ERD: Event related desynchronization.

ERP: Event-related potential.

ERS: Event related synchronization.

ERSP: Event-related spectral perturbation.

FFT: Fast Fourier transform.

FIR: Finite impulse response.

fMRI: Functional magnetic resonance imaging.

GTO: Golgi tendon organs.

HOV: Homogeneity of variance.

IC: Independent component.

ICA: Independent component analysis.

IPA: Intraparietal sulcus.

LED: Light emitting diode.

LOC: Lateral occipital complex.

LPO: Lateral parietal operculum.

M: Mean.

MECD: Ministerio de Educación Cultura y Deporte.

M-I: Primary motor cortex.

PCA: Principal component analysis.

PMA: Pre-motor cortex.

POC: Parieto-occipital complex.

RDT: Repetition Discrimination Task.

RT: Reaction time.

SD: Standard deviation.

S-I: Primary somatosensory cortex.

S-II: Secondary somatosensory cortex.

SMA: Supplementary motor cortex.

SMR: Sensorimotor rhythm.

TMS: Transcranial magnetic stimulation.

TPJ: Temporo-parietal junction.

UNED: Universidad Nacional de Educación a Distancia.

WMA: World Medical Association.

FIGURE LIST

CHA	DT	CED	2
$U\Pi A$	ו או	IKK	Z

Figure 1. An illustration of the classical grouping principles proposed by the Gestalt psychologists to account for the way in which elements are perceived together as part of larger objects......pag. 44.

CHAPTER 3

Figure 1. A schematic view of the pathway followed by the haptic input......pag. 63.

Figure 2. Sensory receptors of the human skin.....pag. 64.

Figure 3. A schematic view of the dorsal (left) and ventral (right) pathways of the somatosensory system responsible for haptic perception and control of movement......pag. 72.

CHAPTER 5

Figure 1. Left: A horizontally oriented pattern grouped by texture-similarity. Right: A vertically oriented pattern grouped by proximity.....pag. 95.

Figure 2. Left: mean reaction times for vertical and horizontal patterns grouped by proximity and by similarity. Right: percentage of errors as a function of pattern orientation and type of grouping. Error bars represent the standard error of the mean over participants......pag. 98.

CHAPTER 6

(A) and percentage of errors (B) in the orientation detection task. Mean response time grouping type. Error bars represent the standard error of the mean (SE) over participants
Figure 3. Characteristics of the 5 IC-clusters of interest. Scalp maps, number of participants and constituent ICs, dipole locations, cluster centroid coordinate (Talairach & Tournoux, 1988), and power spectra for the 5 IC clusters of interest From top-left to bottom right: a) left sensoriomotor, b) right sensoriomotor, c) less parietal, d) right parietal, e) occipitation of the first parietal, pag. 130
Figure 4 . ERSPs of the 5 IC-clusters of interest. Mean log-ERSPs (8-25 Hz) relative to stimulus onset (0) of the IC-clusters of interest for proximity (first column) and similarity (second column) conditions in the orientation detection task, along with uncorrected (third column) and cluster corrected (fourth column) <i>p</i> values. From top to bottom: a) left sensorimotor, b) right sensorimotor, c) left parietal, d) right parietal, e) occipital
CHAPTER 7
Figure 1. a) A view of the Haptic monitor; b) schematic representation of the touch-sensitive individual elements used in the haptic displayspag. 161
Figure 2. Representation of displays for all the conditions in Experiment 1: (1) n grouping; (2) proximity only; (3) texture similarity only; (4) cooperation betwee grouping principles, and (5) competition between grouping principlespag. 163
Figure 3. a) Transformed ratings for each grouping condition (the bars represent ±1 SE); b) normalized effect sizes used to examine the compatibility of the present data with additive effects of grouping principles (Kubovy & van den Berg, 2008 Cooperation between principles is identified by (o) and competition between principles is identified by (o) and competit
Figure 4. Mean response times in ms (a) and error rates in % (b) for directe attention and grouping conditions. The error bars represent ±1 SEpag. 177
Figure 5. Normalized effect sizes used to examine the additivity of the data from Experiment 2. Cooperation between principles is identified by (o) and competition by (÷). The grouping cue on the left is the attended one, and the grouping cue of the right is the non-attended one. Positive scores indicate interference and negative scores facilitation

CHAPTER 8

Figure 1. Left: An overall view of the Haptic monitor. Right: Schematic representation of the individual touch-sensitive elements that formed the haptic displayspag. 202.
Figure 2. Representation of the three experimental conditions used in Experiment 1: (1) Similarity acting alone; (2) cooperation between grouping principles, and (3) competition between grouping principles. The circles inside the box are the target stimuli
Figure 3 . Left: Mean RTs (ms) for the three grouping conditions when the 3 relative target positions were collapsed. Right: Mean RT (ms) for the three grouping conditions corrected for the absolute target position (the bars represent ±1 SE)pag. 211.
Figure 4. Average scalp maps, dipole source location in average brain images (the red dot represents the cluster centroid), Talairach coordinates and power spectra of 5 IC clusters from 19 subjects. (A) Left sensorimotor (n=14); (B) right sensorimotor (n=16); (C) right pre-frontal (n=25); (D) left occipital (n=14) and (E) right parietal (n=16)pag. 214.
Figure 5 . Average event-related spectral perturbations (ERSP) of the five IC clusters selected for further analysis in the three grouping conditions of Experiment 1. From top to bottom: left sensorimotor, right prefrontal, left occipital and right parietal
Figure 6. Representation of all the experimental conditions used in Experiment 2: (1) proximity acting alone, (2) cooperation between grouping principles, and (3) competition between grouping principles. The bottom two rows of each condition represent the catch trialspag. 220.
Figure 7 . Left: Mean RT (ms) for the three different grouping conditions. Right: Mean error rates (%) for the three grouping conditions (the bars represent ±1 SE)pag. 223.
Figure 8. Normalized effect sizes used to examine the additivity of the data from Experiment 2. Cooperation between principles is identified by (o) and competition by (÷). The grouping cue on the left is the task-relevant one, and the one on the right non-relevant (interfering). Positive scores indicate facilitation and negative scores interference

Figure 9. Average scalp maps, dipole source location in average brain images (the red dot represents the cluster centroid), Talairach coordinates and power spectra of 5 IC clusters from 22 subjects in Experiment 2. (A) Left sensorimotor (n=18); (B) right sensorimotor (n=18); (C) right pre-frontal (n=17); (D) left occipital (n=28); (E) right parietal (n=35)......pag. 227.

Figure 10. Average event-related spectral perturbations (ERSP) of the five IC clusters selected for further analysis in the three grouping conditions of Experiment 2. From top to bottom: left sensorimotor, right sensorimotor, right prefrontal, left occipital and right parietal......pag. 229.

TABLE LIST

CHAPTER 3
Table1. Characteristics and functions of the four mechanoreceptor populationspag. 67.
CHAPTER 7
Table 1. Summary of statistics for the different grouping conditionspag. 167
Table 2. Experiment 1. Inferences about the compatibility of the data with additivity of grouping
Table 3. Mean response time (ms) and standard deviations (in brackets) for each condition in Experiment 2pag. 177.
Table 4. Inferences about the compatibility of the data from Experiment 2 with additivity effects of groupingpag. 180
CHAPTER 8
Table 1 . Experiment 1. Mean response times as a function of grouping condition for both relative and absolute target positionspag. 212.
Table 2. Experiment 2. Mean response times as a function of grouping conditionpag. 223
Table 3. Inferences about the compatibility of the data from Experiments 1 and 2 with additivity effects of grouping

CHAPTER 1: PERCEPTUAL ORGANIZATION

1. The problem of organizing the world

When we look at the world around us, we might notice that it is populated by complex and meaningful objects including buildings, animals, trees, furniture and people, all of which are surrounded by background (Palmer, 1999). However, we reach this representation of the world through the brightness, colors, tones, odors, textures and temperatures acquired by the sensory receptors that compound the raw information of our sensations (Kimchi, Behrmann, & Olson, 2003; Palmer, 1999, 2003; Pomerantz & Kubovy, 1981; Wagemans, 2016). The essential process that leads from this raw information to our final "view" of the world around us is what we call perceptual organization. In short, it refers to the task that confronts our perceptual system with deciphering the massive incoming sensory information in order to achieve a veridical, congruent and useful representation of the external environment (Kimchi et al., 2003; Pomerantz & Kubovy, 1981). Consider, for example, the retinal input of the visual system that conform a "retinal mosaic" made up of the sum of the individual activations of each receptor. We can consider this mosaic as a numerical array in which each cell represents the response (in terms of neural activation) of each receptor (Palmer, 2003). The key issue faced here by the visual system is to determine the implicit structure of the retinal image, or in Palmer's words (1999, p 255): "to structure the bits and pieces of visual information that are available in the retinal image, into larger units of perceived objects and their interrelations". Perceptual organization is so closely linked to our conscious perceptual experience that it is easy to forget how complex the underlying process is, given the ambiguities, noise and processing limitations of the human perceptual system. But even with these tremendous limitations, perception is not only possible, but also accurate and stable (Palmer, 1999).

When talking about perceptual organization, two main questions arise. The first question is why perception is organized the way it is. The short and naïve answer to this question is that perceptual organization only reflects the structure of the world that is relevant to the survival of the organism (Palmer, 1999). According to this, the world, or at least part of it, consists of surfaces and objects distributed through the space, and the human perceptual system just reflects this underlying structure. The main problem with this point of view is that the perceptual system does not have direct access to the world (the distal stimulus), but only to the projected retinal image (the proximal stimulus). Therefore, the only way to acquire the environmental structure is through the activation pattern generated by our sensory receptors (e.g., the array of light intensity values that form the retinal mosaic), which contains an infinite variety of possible organizations. A possibly answer to the question of how the perceptual system acquires the structure of the world, is that our perceptual system has evolved to reflect the structure of the environment that is relevant to the survival of the organism (Palmer, 1999). However, it leaves the mechanisms and the factors that underlie the organization of our perceptual experience unexplained. In other words, it does not address the second question about perceptual organization: how it is built over time during the perceptual process. The next sections will be devoted to describing this process.

2. Four different approaches to perceptual organization

Palmer (2003), described 4 different theoretical approaches that have tried to understand the perceptual organization phenomena. The first two were related with the information rationale underlying perceptual organization. The last two

addressed the different levels of explanation.

2.1. The Gestalt psychology (structural simplicity)

The first, and maybe the most relevant theoretical framework that focused on the organizational problem was the Gestalt psychology approach. The key to understanding the perceptual organization problem from the Gestalt perspective was the notion of structural simplicity. They thought that structural simplicity was the guiding principle behind perception, a concept that was embodied in the principle of *Prägnanz* (Wertheimer, 1910, 1923). This principle is described as the tendency of the perceptual system to structure our perceptual experience following the best, most regular and simplest form. This claim has two main implications: 1) perception will seize on and eliminate regularities and redundancies in the perceptual scene; and 2) certain distortions or missing information will be introduced to simplify the final representation. Therefore, the principle of *Prägnanz* can be understood as the process of selecting the most parsimonious possible interpretation about the environment (Pomerantz & Kubovy, 1981). Gestaltists never developed the concept of *Prägnanz* into a welldefined scientific theory. Instead, they refined the general law by writing down several principles that, hypothetically, allowed to predict how the incoming sensory information will be structured by the perceptual system. These principles, often called Gestalt laws (Wertheimer, 1923), add additional constraints to the raw sensory input to minimize complexity or maximize structural simplicity. The basic idea behind these principles is that the elements that share some features like color, motion or spatial distance are seen as belonging to same object because this organized structure is simpler than the independent elements (Palmer, 2003). Unfortunately, Gestalt psychologists established their principles only

phenomenological demonstration without any formal experiment, arguing that those were the kind of features to which the physiological mechanisms of the perceptual system were sensitive. This lack of experimental rigor led to a severe criticism from the psychophysics and behaviorism fields that ended with the vanishing of the Gestalt school.

Nevertheless, and despite this criticism, the Gestalt agenda did not disappear from the field completely, as some of their proposals have been incorporated into the paradigms of information-processing and cognitive psychology. Particularly, the concept of holism has been revisited from several contemporary formulations, resulting on different operational concepts like integral dimensions, emergent features, configural superiority, global precedence and/or primacy of configural properties. In addition, the concept of *Prägnanz* has also been addressed from different theoretical approaches like dynamical systems, Bayesian models, and structural information theory (Wagemans, Elder, et al., 2012; Wagemans, Feldman, et al., 2012).

In sum, even after its disappearance, the questions raised by the Gestalt school more than one hundred years ago continue to generate a large body of research, although the conceptual framework and the methodology used have greatly changed.

2.2. The ecological point of view

The ecological approaches are interested in why our perception structures the world in the way it does. The answer to this question is that perceptual systems just reflect the structure of our environment (Gibson, 1979). According to this, the rationale behind the ecological approach to perceptual organization is to determine what pieces of information go together in the way that best reflects

what actually happens in the world around us (Palmer, 2003).

The main question that an ecological approach to perceptual organization must answer is how does the organism get information about the external world? This is a puzzling question because the organism only has access to internal evidence acquired through the sensory systems, and there is no unequivocal way to know if it really reflects the external world accurately. The only possible answer to this question, is that the correspondence between the environmental information and the organism is grounded on the evolutionary process. Thus, at least some part of the information about the external world would be innate (Spelke, 1990).

Ecological theories of perceptual organization also face a second, *ontological* problem. They assume that there is a unique real structure in the world, and that our senses are capable of revealing it. However, is much more probable that many possible organizations coexist and that the one we perceive is the one with the greatest biological utility for our species. From this point of view, the objects we perceive are not the cause of our perception but its result, an ecological construct that resides in the interaction between the organism and the environment, rather than purely physical entities (Palmer, 2003).

2.3. Computational models

As mentioned above, structural simplicity approaches are interested in how the perceptual system selects among alternative organizations using the available information, whereas ecological ones are interested in the evolutionary utility of the specific organization we perceive. The computational accounts, on the other side, are independent from the previous approaches and deal with the language in which the different theories can be built. According to Marr (1982), the

computational theories can be broadly divided into two different levels: the macro level (the overall architecture) and the micro level (the specific mechanisms).

Computational theories at the macro level, analyze the possible architectures that can account for the world's structure that we see. This usually involves to state the goal of the computation and decompose the global organizational process into simpler sub-processes (e.g. Palmer & Rock, 1994). At the micro level, the focus is on the particular algorithms or computational elements and their interactions. The main goal of these approaches is to identify an adequate representation for the initial (input) and the final state (output) of the organizational process and to implement an algorithm responsible for transforming one into the other (e.g. Kienker, Sejnowski, Hinton, & Schumacher, 1986).

2.4. Neural approaches

The last way to conceptualize perceptual organization is to describe the neural events that are behind the organizational problem. The neural implementation approaches are intimately related to computational approaches, as their main goal is to describe how a particular architecture or algorithm can be implemented in the physical structure of the organism (Palmer, 2003). Moreover, they act as a logical constraint to those models as no computational model could be plausible without being embodied in the specific hardware in which it is meant to operate. Examples of this kind of approach include single-cell recording, functional brain imaging, neuropsychological studies of patients with brain damage and any methodological tool that deepens into the physiology of the nervous system (Palmer, 2003).

CHAPTER 2: PERCEPTUAL GROUPING

Haptic Perceptual Grouping: Behavioral and Neurophysiological Correlates

1. The grouping processes

Perceptual grouping has been closely related to perceptual organization although they are not synonymous. In fact, perceptual grouping is a particular kind of organizational process, one that determines the qualitative elements of our perception. Shortly, it consists in the perception by the observers of some elements of the perceptual field as going together more strongly than others (Wagemans, Elder, et al., 2012). The importance of grouping processes can be illustrated if we imagine a display composed of several elements. The number of possible subsets in which we can divide the display grows exponentially with the number of elements. However, for a given configuration, we only perceive one of those subsets at a time and usually the first we perceive is the only one (Palmer, 1999).

This problem was firstly introduced by Wertheimer (1923) when studying the stimulus factors that affect how the discrete elements in a complex display are perceived as going together or belonging to each other. Wertheimer addressed the problem by constructing arrays of simple elements and varying the relations among them in an attempt to establish which features caused some elements to be grouped with others (Palmer, 1999).

2. The grouping principles

Wertheimer's investigations led him to describe a set of principles which he called *laws of grouping*, that, "all else being equal", determined the objects and parts the observers perceived in the environment. The evidence presented to support these grouping principles was purely phenomenological; thus, the classical grouping principles were firmly established by demonstration, without any formal

experimentation. After decades without any significant progress in the number or nature of the grouping principles, recent advances have proposed a new set of additional grouping principles that complement the ones postulated by the Gestalt psychologists (Alais, Blake, & Lee, 1998; Palmer, 1992; Palmer & Rock, 1994). In the following sections, we describe both *classical* and *new* grouping principles in turn.

2.1. Classical grouping principles

In his first demonstration, Wertheimer employed a line of equally spaced dots. When the spacing between some adjacent dots was altered so that some dots were closer to each other and others were farther away, the closer ones tended to strongly group together (Palmer, 1999). Wertheimer called this grouping effect caused by the relative closeness of the individual elements **proximity**. After this first demonstration, Wertheimer illustrated many other grouping principles. The principle of **similarity**, for example, states that all else been equal, the most similar elements tend to group together. Similarity, therefore, can be considered a general principle that covers several different features and/or properties of the individual items like color, size, orientation, brightness, texture and temperature (Palmer, 1999). Even proximity can be considered as a special case of similarity, one in which the underlying similar dimension is the position of the elements. However, even though all these features are usually considered as part of same general principle of similarity, not all are equally effective in producing grouping effects. In fact, different sensory systems seem to be more sensitive to different kinds of similarity. Another grouping factor refers to the fact that when the individual elements move in the same direction and at the same rate, our perception associates the movement as being part of the same stimulus and, then, the elements tend to be grouped together (Palmer, 1999). Wertheimer (1923) named this effect as **common fate**.

Other grouping principles influence the perception of line-like elements. In this line, the **good continuation** principle states that elements that can be seen as a smooth continuation of each other tend to be grouped together. This allows the observers to perceive single uninterrupted objects when intersections and/or visual overlaps are present. The principle of **closure**, on the other hand, refers to the tendency of observers to group the elements that form a closed figure (sometimes overriding good continuation), even if the picture is incomplete, partially hidden by other objects or some information is missing. Finally, other factors like **symmetry** and **parallelism** also influence the way observers group the individual elements of the perceptual scene (Palmer, 1999). Figure 1 summarizes the classical principles of perceptual grouping along with phenomenological examples of each of them.

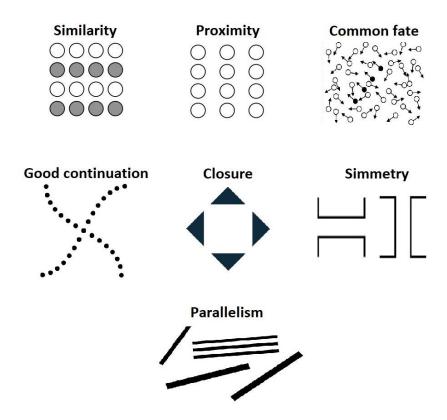


Figure 1. An illustration of the classical grouping principles proposed by the Gestalt psychologists to account for the way in which elements are perceived together as part of larger objects.

2.2. New grouping principles

After the Wertheimer's proposal, no other grouping principles were described in the following years. Recently, however, a new set of 5 grouping principles has been proposed: *generalized common fate* (Sekuler & Bennett, 2001), *synchrony* (Alais et al., 1998), *common region* (Palmer, 1992), *element connectedness* and *uniform connectedness* (Palmer & Rock, 1994).

The principle of **generalized common fate** is an extension of common fate to luminance changes. This principle states that when the elements of the perceptual scene become brighter or darker at the same time (even if each single element have different luminance levels), observers tend to group those elements together. It is possible that the principle of common fate operates not only through the 3-

dimensional physical space, but also through luminance space or even other feature spaces. In a broad sense, it can be considered as another form of similarity, but based on the similarity of the changes in feature values instead of the similarity of the feature itself (Wagemans et al., 2012).

Similarly to the generalized common fate principle, **synchrony** is the tendency of perceiving elements that change simultaneously as going together. However, these changes do not have to go in the same direction (as they do in generalized common fate). Grouping by synchrony emphasizes that the elements that belong to the same object in our environment tend to change simultaneously, reflecting a strong temporal regularity in our surrounding events (Alais et al., 1998; Palmer, 1999).

Grouping by **common region**, refers to the tendency of the elements that are located within the same bounded region of the space to be grouped together. The rationale behind this grouping principle is that the elements within a closed area share the topological property of being contained by a larger contour, a situation that usually means that the elements are parts of the surface of a single object, rather than independent objects (Palmer, 1992).

The fourth newly proposed grouping principle is **element connectedness** that refers to the fact that distinct elements that are connected or share a common border with other elements tend to be grouped together. The elements bounded by means of this grouping factor share the topological property of connectedness, which could be seen as an extreme case of proximity. However, Palmer and Rock (1994) argued against this conceptualization based on topological and phenomenological reasons. The rationale behind this grouping principle is that

elements that are physically connected in the space are usually part of the same object (Palmer, 1999; Peterson, 1994).

Finally, **uniform connectedness** refers to the principle by which the perceptual system makes an initial partition of the scene into a set of exclusive regions with uniform properties (luminance, color, texture, motion, etc.). This grouping principle would be responsible for the formation of the primary units that constitute the input for the other grouping processes. However, even though similar processes have been widely assumed by theories of computational vision (Marr, 1982), this characterization of the uniform connectedness as responsible for the initial partition of the scene has not been always accepted (see Kimchi, 2000; Peterson, 1994).

3. Methodological approaches to the study of perceptual grouping

The methods employed to study perceptual grouping since the early days of the Gestalt psychology can be broadly divided into two different types. The first method involves phenomenological demonstrations and behavioral reports of specific aspects of the phenomenology. This includes qualitative introspective experiences, subjective judgments and subjective ratings. The second approach includes tasks that focus on objective aspects of perception yet remain sensitive to grouping effects. This includes psychophysical directed attentional tasks along with indirect tasks in which participants are not aware of the grouping processes. In the following sections, we will describe both methodological approaches in detail.

3.1. Phenomenological (subjective) methods

The **phenomenological demonstrations** introduced by Wertheimer (1923) were the first instrument historically employed to establish the validity of the principles that are thought to influence perceptual grouping. They have been widely used by other Gestalt and cognitive psychologists (Kanizsa, 1976; Palmer & Rock, 1994). These phenomenological demonstrations are based on the following reasoning: if the observers of the displays agree with the phenomenological description provided by the experimenter, it means that the observers show the effect, and the validity and relevance of the factor that has been manipulated in the demonstration is established. The advantage of these demonstrations is that they give to the observer a direct experiential feeling and provide the very definition of the phenomenon under scrutiny, in a way that is not under the reach of other experimental methods (Palmer, 2003). Nevertheless, the phenomenological demonstrations have often been criticized due to their serious drawbacks and the lack of rigorous experimental procedures compared to behavioral oriented research. The first drawback is that their qualitative nature does not generate numerical data. In fact, not all the observers show the predicted effects. However, as they are not counted in any way, it is not possible to know how generalized this absence of grouping in the general population is. In the same way, it is not possible to compare the size of the different organizational effects and use the data to test quantitative theories.

A second problem with this approach is that the effectiveness of these methods is restricted to robust organizational effects. When ambiguity appears, the solely phenomenological demonstration does not suffice. Finally, an inherent problem closely linked to phenomenological demonstrations is that they rest on

subjective foundations. There are no correct/incorrect grouping effects. In contrast, there is just a purely personal experience of what the observer perceives. This leaves the situation open to uncontrolled bias and strategic effects derived from the experimental instructions and/or the previous knowledge about what the observers are supposed to experience (Palmer, 2003). Due to these limitations, purely phenomenological methods are not suitable instruments for complex experimental analyses of grouping phenomena.

To overcome some of the problems of the phenomenological demonstrations, the experimenter can simply ask the observers to provide overt behavioral judgments of an aspect of their phenomenological experience. In the quantified behavioral reports of phenomenology, the proportion of perceivers who report one of two possible organizational outcomes can be used as a quantitative measure of the strength of grouping due to the experimental manipulations of the factors involved (Rock, Nijhawan, Palmer, & Tudor, 1992). This allows the experimenter to compare the effect sizes of different combination of factors and introduce the results into quantitative models for testing (Kubovy, Holcombe, & Wagemans, 1998; Kubovy & Wagemans, 1995). However, it is important to note that the subjective basis of the introspective reports cannot be solved, as they are still based on a phenomenological experience that has no objectively correct answer. Performance-based measures of subjective grouping are, therefore, not possible as there is no organizational standard to compare to. In order to obtain performance measures, we must change the object of study from subjective experience to something qualitatively different.

3.2. Psychophysical (objective) methods

To solve the subjectivity problem of the phenomenological reports, we can ask

the observers to report an objective aspect of perception still sensitive to grouping by transforming the perceptual experience. This can be achieved by either (1) forcing the observers to judge certain aspects of the stimulus, or by (2) hindering their perception. In both cases what the experimenter obtains is an indirect measure of the grouping effects (Palmer, 2003).

The simplest psychophysical method to obtain an indirect measure of grouping is to arbitrarily define a correct response corresponding to a given organization. Then, the observers must attend to this particular configuration while ignoring other possible alternatives. In this case, the observers are still aware of the grouping task. However, it does not involve the spontaneous organization attained by the observers during the perceptual process, but the perception of a previously defined organization. In this case, the measure is not a quantified phenomenological report, and engages mechanisms not involved in the natural perception of the scene. These methods, called **directed attention objective methods**, have been implemented in multiple tasks in which participants had to identify the orientation of dot arrays (Han, 2004; Han, Ding, & Song, 2002; Karhu & Tesche, 1999; Schmidt & Schmidt, 2013) or indicate the side with which a central target was grouped (Luna, Villalba-García, Montoro, & Hinojosa, 2016), according to a previously defined grouping factor.

It is key to mention that the method just described eliminates the possibility of spontaneous grouping without explicit knowledge about what should be perceived. Thus, this method could lead to the use of alternative strategies not related to grouping itself (Kubovy & Gepshtein, 2003). This problem could be avoided by using **objective indirect methods**, in which the observers are not aware (not directed attention) of the grouping manipulations. One example of this

objective and indirect method is the Repetition Discrimination Task developed by Palmer and Beck (2007). This task provides an indirect measure of grouping that does not require explicit attention to the grouping itself. In this task, observers are presented with a linear array of elements that alternate in a given feature (e.g., size, color, texture, etc.) except for a pair in which the feature is repeated. The observer's goal on each trial is to identify whether the repeated pair is composed of one or another value of the key feature (e.g., square/circle, red/blue, smooth/rough). The responses are measured in three different conditions: (1) in the within group trials (cooperative condition), another grouping factor (e.g. proximity) biases the target pair to be perceived as being part of the same group; (2) in the between group trials (competitive condition), the grouping factor biases the target pair to be perceived as part of two different groups. Finally, (3) in the neutral trials (acting alone condition), the grouping factor does not bias the targets in one-way or the other. Thus, the objective indirect methods provide a quantitative measure of grouping while preventing the strategic effects of directed attention tasks.

Objective measures have several advantages over phenomenological tasks, among which the most significant is the measurement of objective performance. However, they also have important drawbacks, especially the indirect measure of subjective organizational effects. The only way to avoid the limitations of each task is the use of a convergent approach based on multiple methods to investigate the perceptual organizational effects. This combination of methods has been a very fruitful strategy to study perceptual grouping, especially in reference to the laws that govern grouping in an environment in which multiple grouping factors act simultaneously.

4. The laws of grouping: how do grouping principles interact?

The Gestalt psychologists failed to develop a complete and meaningful theory of perceptual grouping due primarily to two related reasons. The first reason is that they focused almost exclusively on phenomenological demonstrations. The second reason is the lack of quantification of their data, which is also a direct consequence of the first (Kubovy et al., 1998). For example, phenomenological observations can be used to state that the strength of proximity decreases with distance and the strength of similarity decreases with dissimilarity. However, for any given value of distance and similarity, it is not possible to know which is stronger, and therefore, we cannot predict which grouping principle will prevail or what is the resulting strength of the combined cues. To do so, it is compulsory to develop a function that relates grouping strength to grouping features like distance or similarity. This function is necessary to predict what the result of the grouping process will be in realistic situations when more than one grouping principle is working at the same time.

This problem is better captured by the following situations: If two (or more) grouping principles tend to produce the same perceptual organization, how much stronger is this organization compared to the resulting organization of each principle alone? In the same vein, if two (or more) grouping principles tend to produce different perceptual organizations, how much weaker is the resultant percept and which principle will prevail? The problem can be reformulated in the following words: when grouping principles act conjoined, are their combined

strengths less, equal or greater than the sum of their individual strengths? (Kubovy & van den Berg, 2008).

The topic was first addressed by Koffka (1935/2013), who thought of grouping as caused by attraction forces between the members of the group and concluded that Gestalts are non-additive emergent percepts and, therefore, the algebraic notion of addition was meaningless in this context. However, later works developed from the experimental psychology paradigm have shown that the conjoined effect of grouping principles can be explained by an additive model in which the total grouping strength equals the sum of the individual strengths produced by each principle alone (Kubovy et al., 1998; Kubovy & van den Berg, 2008; Kubovy & Wagemans, 1995).

4.1. Grouping quantification strategies

To define the rules that govern the conjoined action of different grouping factors it is necessary to measure the strength of each grouping principle and to determine how these strengths are combined into a single percept. To this end, researchers have followed two different strategies. The first is called the trade-off strategy, while the second is known as the proximity-first strategy.

4.1.1. The trade-off strategy

As its own name suggests this strategy investigates the trade-offs between pairs of grouping principles. It consist of measuring the strength of grouping principles while simultaneously determining how both strengths are combined (Kubovy & van den Berg, 2008). There are two complementary ways to do this: (1) for each proximity level, a similarity level is found such that the probability of seeing a proximity grouped pattern and a similarity grouped pattern is the same; (2) for each similarity level, a proximity level is found such that the probability of

perceiving a similarity grouped pattern and a proximity grouped pattern is the same. The result of both methods is a *grouping operating characteristic* curve (GOC) that shows the trade-off between both grouping principles in the same way as traditional attention operating characteristics curves (AOC) show the trade-offs between attentional resources. The fundamental difference is that GOCs are controlled by the stimulus and not by the person's choice of attentional allocation.

The first systematical attempts to study the interaction between grouping principles using the trade-off strategy correspond to Rush (1937), Hochberg & Silverstein (1956), and Hochberg & Hardy (1960). These authors employed dimotiff and split lattices in which grouping by proximity and similarity could organize the array in opposite directions. The participants' task was either to indicate the orientation of a sequence of different lattices, or to adjust proximity (vertical/horizontal) so that the strength of grouping by proximity and similarity was in equilibrium. Four decades later, Quinlan and Wilton (1998) developed an innovative different approach to study the interactions between grouping principles. They used strips of seven elements in which the central element was the target. These researchers manipulated the proximity and similarity of the central target with respect to the right and left surrounding elements, and asked the participants to rate the degree to which the central target grouped with the elements on the right or on the left under three different conditions: a) cooperative conjoining, in which both grouping principles strengthen grouping on the same side; b) competitive conjoining, in which each grouping principle tend to group the target on opposite sides; and c) acting alone grouping cues. Finally, Claessens and Wagemans (2005) tried to produce a complete GOC map using a new type of lattice, the Gabor lattice, in which dots were replaced with Gabor or Gaussian

patches. They asked the observers to indicate the direction along which they saw the lattice organized. The combined results of this work and those obtained in previous research showed a clear pattern; when pairs of grouping principles act conjoined within the same perceptual scene, they trade-off against each other following a clear additive function. However, the trade-off strategy has some drawbacks that preclude obtaining a complete GOC map. In the next section, we describe the *proximity first strategy*, which allows to construct complete GOC maps and obtain complementary measures of the strength of grouping principles (Kubovy & van den Berg, 2008).

4.1.2. The proximity-first strategy

In this strategy, the researcher first measures grouping by proximity and then includes other grouping principles to measure the relation between them and proximity (Kubovy & van den Berg, 2008). The *proximity-first strategy* provides us with more information about the strength of grouping principles and their interactions, since it allows us to know not only if one principle is stronger than other, but also informs us about how much stronger it is, by constructing complete GOC maps with different pairs of grouping cues.

The first investigator to use this strategy was Oyama (1961), who measured the strength of grouping by proximity on its own using rectangular dot lattices. Oyama, recorded total amount of time the observers informed seeing the vertical and horizontal organizations. The data showed that the ratio of the time participants saw vertical and horizontal organizations and the ratio between the horizontal and vertical distances are linearly related. Later, Kubovy and Wagemans (1995) used brief exposures to dot lattices in which the principal directions were not always perpendicular. Using this method, they obtained a linear function

(proximity attraction function) that constitutes a quantitative law of proximity attraction, which depends on the relative interdot distances and its invariant over distinct lattices: a *pure distance law* (Kubovy et al., 1998; Kubovy & van den Berg, 2008). Finally, Kubovy and van den Berg (2008) employed dot lattices in which they manipulated relative proximity and luminance similarity to determine the relation between the conjoined strength of the grouping principles and the strength of each principle in isolation. Their results showed that the grouping principles under study act as a linear system in which the conjoined grouping strength equals the sum of the individual effects.

Taken together, the above reviewed research showed convergent evidence around the additive nature of the grouping principles. However, several questions should be addressed before the proposed additive model can be taken as generally valid. Other grouping principles, combinations between them, and different sensory modalities must be tested to draw solid conclusions.

5. Neural mechanisms of perceptual grouping

The initial formulations of the Gestalt theory conceived the brain function as derived from the activity of dynamically converging electromagnetic brain fields (Köhler & Wallach, 1944). Later studies failed to prove its key predictions (Lashley, Chow, & Semmes, 1951). The evidence supporting a brain architecture consisting of highly organized and interconnected neurons that form complex circuits with selective responses to different properties of the external stimulation was weak. This supposed a hard blow to the Gestalt's conception of brain mechanisms (Wagemans, Elder, et al., 2012). However, even though the current view of brain perceptual mechanisms is far from Kohler's conceptualization, the

modern neuroscience has addressed the Gestalt questions about the implementation of the perceptual organization in the human brain in at least four different topics: the neural correlates of the different grouping principles, contour grouping, figure-ground organization, and border-ownership assignment.

5.1. Neural correlates of grouping principles

Research addressing the brain correlates of Gestalt principles has mainly focused on grouping by proximity and similarity within the visual system. In two similar ERP studies, Han, Song, Ding, Yund, and Woods (2001), as well as Han et al. (2002), used rectangular dot arrays defined by the spacing between elements and shape similarity to investigate the neural mechanisms of proximity and similarity grouping. Their results showed that proximity grouping was associated with a short-latency enhanced positivity (Pd110) over medial occipital cortex and right parietal enhanced negativity (Nd230). Grouping by shape similarity, in contrast, was only reflected in a longer-latency, left lateralized occipito-temporal negativity (Nd340). These different neural origins and time courses suggest an earlier clustering of the elements based on spatial parsing that agrees with the faster behavioral responses to proximity grouping. The different scalp and hemispheric distributions also suggest that right dorsal and left ventral pathways are preferentially involved in proximity and similarity grouping, respectively. This proposal is consistent with the involvement of the right dorsal occipito-parietal stream in the processing of spatial features and low spatial frequencies, and the role of the left ventral occipito-temporal stream in the processing of object features and high spatial frequencies (Kitterle, Christman, & Hellige, 1990; Ungerleider & Haxby, 1994). Researchers have also investigated the interactions between proximity and similarity when both grouping principles are conjoined into congruent or incongruent configurations. Particularly, Han (2004) conducted an ERP study using rectangular dot arrays and found that the first sign of interaction between grouping principles appeared at the N1 component (180-220 ms) over posterior temporo-parietal areas. The amplitudes of this component in the similarity condition were lower when incongruent proximity cues appeared within the same stimulus. Nevertheless, proximity was not affected by the congruency of similarity cues. Thus, it seems that spatial relations between local elements based on proximity provide an initial cue for segmenting the perceptual field and interfering over similarity-based organizations that are involved only at a later stage.

5.2. Neural correlates of other organizational phenomena

One of the earliest demonstrations of perceptual organization correspond to the **illusory contours** (Schumann, 1904). The Gestalt psychology explained the existence of these contours by completion process in the visual cortex. Von Der Heydt, Peterhans, and Baumgartner (1984) investigated this phenomenon recording single neuron responses in monkeys and found illusory contour responses in the V2 area of the visual cortex that were stimulus driven. A parsimonious model that account for this findings proposes that V2 activity reflects a general mechanism for the detection of occluding contours based on the presence of luminance/color edges and occlusion features (Heitger, von der Heydt, Peterhans, Rosenthaler, & Kübler, 1998), which could be considered an implementation of the completion principle.

The spatial limits of the illusory contours make it easy to explain within the limits of the receptive fields of the neurons of the visual cortex. However, other phenomena such as **figure-ground segregation** occur in a much larger spatial

range. Lamme (1995) found enhanced responses of V1 neurons in the monkey's visual cortex for figure regions defining texture, orientation, motion, depth and color. This finding suggests a general mechanism implemented in the primary visual areas. In the image, foreground and background are adjacent regions, which share occluding contours. The information about these contours must be assigned unilaterally to the figure or the ground; thus, a closely involved process in figure-ground organization is the **border-ownership assignment**. How border-ownership is coded by the neurons of the visual cortex was not clear until Zhou, Friedman, and von der Heydt (2000) recorded the firing rate of V1, V2 and V4 orientation-selective neurons in the monkey's visual cortex. The results revealed that these neurons were contour sensitive and their firing rate depended on where the figure was located relative to the receptive fields of each neuron. Therefore, borders are represented by a different group of neurons for each side of the ownership, and the differential activity between the two sides represents the border.

Summing up, from the neurophysiological results reviewed above, we can conclude that the activity of the sensory neurons depends on both, the holistic configuration of the perceptual field and the specific features of the stimulus detected within each receptive field. Even though the earlier postulates of the Gestalt psychologists about the brain function were wrong, the atomistic approach based on feature detectors that was derived from the experiments of Hubel and Wiesel (1959) also cannot provide a complete explanation of how perceptual organization is acquired by the brain. An integrative view of the brain function is needed, emphasizing the role of holistic processes, concurrent networks and context influence, as well as the individual function of single neurons.

CHAPTER 3: PERCEPTUAL ORGANIZATION IN THE SENSE OF TOUCH

Haptic Perceptual Grouping: Behavioral and Neurophysiological Correlates

1. Introduction

The sense of touch is a complex perceptual system that plays a fundamental role in the awareness of the surroundings, the consciousness of self, as well as in thought and action. Since the first systematic experimental investigation conducted by Weber (1795-1878), several scientific disciplines have approached touch from many different directions using a wide variety of methods. The results, however, have not led to a thorough theoretical body. This absence of a theoretical framework contrasts with a huge number of findings pertaining the basic principles of touch and their applications that have taken place in recent years. These findings are due to a renewed interest in the field driven by the development of tactile displays, interface technologies and adapted systems for visually and aurally impaired people (Gallace & Spence, 2011; Grunwald, 2008).

The study of touch from a psycho-physiological point of view includes both the information acquired by cutaneous sensitivity and kinesthesis. The term "haptics" refers to the process of obtaining information about the environment by the active manipulation of the objects, through both, cutaneous sensitivity and kinesthetic information (Lederman & Klatzky, 2009). Unlike vision and audition, two sensory modalities that provide highly accurate spatial and temporal information respectively, the sense of touch, and specially the haptic system, stands out for its effectiveness in processing the material characteristics of surfaces and objects like texture, hardness or temperature. The differences between touch and vision go beyond the features to which each sense is better adapted. They also pertain to the nature of sequential vs parallel processing in touch and vision, respectively, as well as the effects of their respective sensory experiences to other cognitive processes like emotion or memory. Despite these differences, research in touch shares many

of the theoretical issues of other research areas, like the structure of the information acquired and its representational nature, its development along the life span, how the information is processed (serial/parallel processing, holistic/component properties), the laterality and hemispheric specialization (Heller, 2013) and, most relevant for the present study, the perceptual organization and grouping processes.

2. Anatomical and physiological bases of active touch (the haptic system)

When human perceivers manipulate objects, the receptors of the skin, joints and muscles activate. The sense of touch uses the sensory information from the mechanic and thermo receptors of the skin, in conjunction with the mechanoreceptors located in muscles and joints to acquire the haptic input (Lederman & Klatzky, 2009). Then, the information is sent to the central nervous system, where it serves two different functions: 1) the haptic perception (the roughness of a surface, the curve of an object, the hardness of a material and so on); and 2) the control of the movements to ensure stable grasp or complex manipulations (Goodwin & Wheat, 2008) (See Figure 2). In the following sections, we will review the biological basis of touch and, especially, of the haptic perception.

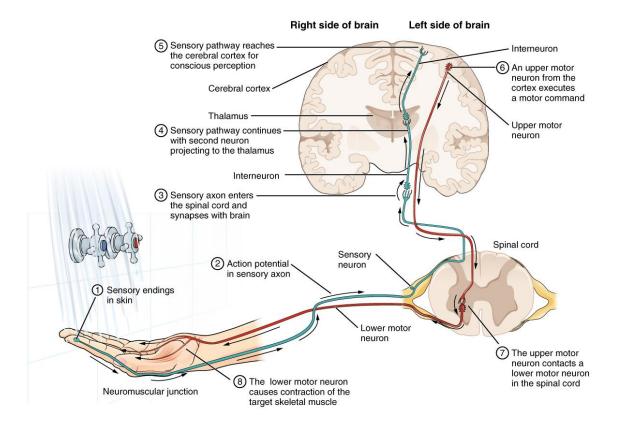


Figure 1. A schematic view of the pathway followed by the haptic input. (Ayrop: OpenStax - https://cnx.org/contents/FPtK1zmh@8.25:fEI3C8Ot@10/Preface, CC BY 4.0, https://commons.wikimedia.org/w/index.php?curid=30147919)

2.1. Mechanoreceptors and their physiological mechanisms

The mechanoreceptors can be categorized into those situated within the muscles and joints, and those located in the skin and subcutaneous tissues, which provide information about the position and movement (see Figure 3). Moreover, within the connective tissue, numerous free nerve endings react to thermal and painful stimuli (polymodal nociceptors), which are terminal points of afferent fibers without any specific structure around them (Grunwald, 2008).

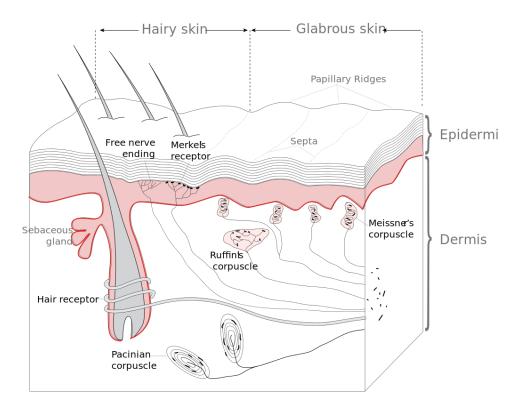


Figure 2. Sensory receptors of the human skin (By Thomas.haslwanter CCBY-SA3.0, https://commons.wikimedia.org/w/index.php?curid=14640652).

2.1.1. Mechanoreceptors of the joints and muscles

The mechanoreceptors of the joints are located within the connective tissue, forming the joint capsule. The first type, the **Ruffini corpuscles** (Slow-adapting type II or SA-II nerve fibers) nerve fibers are located in the external fibrous layer of the joint capsule. They consist of several cylinders formed by perineural cells connected to a myelinated axon, split into several branches, covered incompletely by Schwann cells. Ruffini corpuscles respond with high precision and sensitivity to the stretching of the collagen fibers, and their firing pattern adapts slowly to maintained stimulation. A second type of joint receptor is the **Pacinian corpuscle** (Fast-adapting type II or FA-II nerve fibers). This kind of receptor is formed by terminal glia cells symmetrically arranged in laminae, innervated by a myelinated axon. Pacinian corpuscles are the largest mechanoreceptors found in humans and other mammals, and they respond to vibration stimuli with an optimum sensitivity

of around 200 Hz (Halata & Baumann, 2008).

Two types of mechanoreceptors are found in the musculature. The first are the Golgi tendon organs (GTO), located in the juncture between muscles and tendons. GTOs are spindled shaped, point both towards the muscle and tendon, and are usually innervated by 3 to 6 myelinated afferent axons. Their function is to monitor the tension of the muscle and initiate protective spinal reflexes when this tension exceeds a critical value. The second type of muscle mechanoreceptor is the Muscle spindle. Muscle spindles consist of two (inner and outer) spindle sheaths formed by perineural cells. Two types of muscle fibers surrounded by connective tissue run through the muscle spindles: thin nuclear chain fibers and thick nuclear bag fibers. In addition to the sensory afferent axons, efferent axons from motor neurons also innervate the muscle spindles. Muscle spindles monitor the length and the changes in length of the muscles (Grunwald, 2008).

2.1.2. Mechanoreceptors of the skin

Cutaneous receptors can be found across the body surface in hairy and hairless skin; however, the vast majority of studies have focused on receptors located in the hairless (glabrous) skin. The response characteristics of each type of receptor can be differentiated by the size of their respective receptive fields (small/large) and their adaptation rate (continuous response vs onset/offset response) (Lederman & Klatzky, 2009).

The **Meisner corpuscles** (fast-adapting type I or FA-I nerve fibers) are positioned in the papillary layer, close to the epidermis and adjacent to adhesive ridges. Meisner corpuscles are oval (100-150 μ m x 40-70 μ m) and their longitudinal axis is perpendicular to the skin surface. The corpuscle is composed of terminals from myelinated fibers separated by terminal glial cells, and its

innervated by several myelinated axons (Ide, Kumagai, & Hayashi, 1985). Meisner corpuscles respond to indentation changes (with maximum sensitivity around 20-30 Hz) in the skin, with short and rapidly adapting bursts (Johansson, Landstrom, & Lundstrom, 1982).

The other type of specific cutaneous mechanoreceptor is the **Merkel nerve** ending (Slow-adapting type I or SA-I nerve fibers). Merkel nerve endings are located within the epithelium, in the basal layer of the glandular ridges of the epidermis. They consist of an oval Merkel cell and a discoid nerve terminal. Merkel cells are innervated by single myelinated nerve fiber from the nerve plexus of the dermis. Their function is to respond to the indentation of the skin with long lasting and slowly adapting bursts of action potentials (Halata & Baumann, 2008; Ogawa, 1996).

In addition to the Meisner corpuscles and the Merkel nerve endings, the cutaneous mechanoreceptors also include **Ruffini corpuscles** (Slow-adapting type II or SA-II nerve fibers) and **Pacinian corpuscles** (Fast-adapting type II or FA-II nerve fibers), already reviewed in Section 2.1.1, which respond to lateral skin stretch and temporal changes in skin deformation, respectively. A summary of the different types of mechanoreceptors, their main characteristics and function can be found in **Table 1**.

Table 1. Characteristics and functions of the four mechanoreceptor populations

Mechanoreceptor	Receptive field	Adaptation rate	Sensitivity	Primary function
Slow-adapting type I (SA-I) (Merkel)	Small	Slow	Sustained pressure (very low frequencies < 5 Hz)	Very-low-frequency vibration detection; coarse texture perception, pattern/form detection; precision grasp and manipulation
Fast-adapting type I (FA-I) (Meissner)	Small	Fast	Temporal changes in skin deformation (5- 40 Hz); spatial deformation	Low-frequency vibration detection; precision grasp and manipulation
Fast-adapting type II (FA-II) (Pacinian)	Large	Fast	Temporal changes in skin deformation (40- 400 Hz)	High-frequency vibration detection; fine texture detection; precision grasp and manipulation
Slow-adapting type II (SA-II) (Ruffini)	Large	Slow	Sustained downward pressure; lateral skin stretch; low dynamic sensitivity	Direction of object motion and force due to skin stretch; precision grasp and manipulation; finger position

2.2. The "what" and "where" systems in touch

The renewed interest in touch has opened an interesting debate about the existence (in line with other sensory modalities) of two different subsystems: a system responsible for perceptual and memory functions (the "what" system), and another responsible for the perceptual guidance of action (the "where" system) (Lederman & Klatzky, 2009). The distinction is supported by behavioral and neuroimaging studies that show greater interference between two simultaneous "what" and "where" tasks relative to cross-function tasks (Chan & Newell, 2008), as well as different activations of superior and inferior parietal areas in object localization and object recognition tasks, respectively (Reed, Klatzky, & Halgren, 2005).

The "what" system is responsible for processing the different characteristics of surfaces and objects. The system relies on feature detection carried out by the

peripheral receptors, resulting in a wide spectrum of sensory primitives that constitute the input for object processing. The properties accessible through this system can be broadly divided into two classes: (1) material properties, defined as those independent of the particular object sample; and (2) geometric properties, defined as those that describe the structure of the object sample (Lederman & Klatzky, 2009).

The material property that has received more attention from researchers is the **surface texture** (roughness). It reflects the interaction between the properties of the surface and the exploratory strategy. The principal factor that determines the perceived roughness is the gap between the elements of a surface and, to a lesser extent, the width of those elements (Taylor & Lederman, 1975), while the temporal features seem not to be involved. However, the most accepted model of roughness perception is the "duplex" model. This model differentiates between two different surface scales: above and below 200 microns. Above this point, the spatial characteristics of the texture seem to dominate perception. In contrast, for fine surfaces below this point, texture detection seems to be based on the temporal vibratory signals detected by the Pacinian corpuscles (Bensmaïa, Hollins, & Yau, 2005). From a psychological point of view, Ballesteros, Reales, De Leon, and Garcia (2005) studied the haptic texture space using a spatial arrangement task in which participants explored surface textures and arranged the surfaces so that the distances among them were proportional to their similarity. The results showed that the most salient dimension of the haptic space was smoothness/roughness followed by hardness/softness. They also identified a third dimension called slippery/sticky. Interestingly, the study also showed that the haptic and visual explorations produced similar dimensional maps with nearly perfect correlations

between both modalities. The second material property is the **thermal quality**, or the apparent warmth/coolness of a surface. The thermal perception is the result of the interaction between the skin and the contacted surface. The main signal for the apparent thermal sensation is the difference between the initial skin temperature and the temperature of the skin after contact. In other words, how much the skin temperature changes after contact with the surface (Ho & Jones, 2004). Another material property, the **compliance**, refers to the deformability of the touched object (or surface) under force. This property can distinguish between compliant objects (those that show continuous indentation under pressure) and rigid objects (those that deform the skin and compress it). Compliance is discriminated by the tactile system using the differences in spatial pressure distribution detected by cutaneous mechanoreceptors. The last material property is weight, a property that reflects the density and structure of an object. Although weight can be perceived in a stationary way, introducing movement through active exploration improves the precision of the perceptual judgment, as perceived weight is determined by the resistance of the object to the rotational forces of the limbs (Amazeen & Turvey, 1996).

The geometric properties of an object are those that determine the size and shape of an object. The geometric property that has received more attention in tactile research is the **curvature**, as local shape can be expressed in terms of the local curvature of the object. When skin is pressed against a curved surface, the pressure gradient of the skin is mapped on the fast and slow adapting mechanoreceptors (SA-I and FA-I). Indented surfaces (and edges), on the contrary, activate primarily SA-I mechanoreceptors (Goodwin, Macefield, & Bisley, 1997). Finally, another important geometric property is **orientation**. In line with vision,

vertical and horizontal lines are perceived more accurately than oblique ones (Lechelt, Eliuk, & Tanne, 1976). This effect depends on the gravitational cues available during exploration and occurs late in the orientation processing according to an abstract frame of reference (Gentaz, Baud-Bovy, & Luyat, 2008).

The "where" system in touch, as its equivalent in vision, is involved in the guidance of actions and the description of where surfaces and objects are in the space. However, the tactile localization of the objects can be referred to the body (where the stimulus is applied) or to the external space (where the stimulus that is being touched is) (Lederman & Klatzky, 2009). The main question regarding bodily localization is how people localize the contacts in their own bodies. The main factor that affects the precision of bodily contact localization is the spatial resolving capacity of the skin, which is not uniform through the entire body. Localization is also affected by space-time interactions. Particularly, the temporal interval between equally spaced contacts is known to affect the perceived location and distance between those contacts (Flach & Haggard, 2006).

Regarding the localization of points in space external to the body, research has shown differences between the ability to return to a previously touched location (based on motor memory) and the ability to report where that location was in the external space (based on the representation of the space). In the latter case, there are at least two potential reference frames that contribute to localization. The first is a coordinate system centered on the perceiver's body (egocentric). The second is independent of the perceiver and centered in the spatial relations between the objects (allocentric). The model proposed to account for haptic localization in the external space proposes that perceivers have two different and competing frames of reference; the first is centered on the body

(usually the hand) and the second on the external space. These two frames vary in their relative weights across both tasks and subjects (Kappers, 2007).

2.3. Neural basis of touch

When investigating the neural basis of touch and active behavior, the first step is to understand the afferent types and pathways involved. The second step is to find out how information is represented and coded in the neural responses initiated by the peripheral receptor system. The conjoined action of this system includes the mechanoreceptors of the skin, the pain, temperature and itch receptors, and the afferents located in the muscles, tendons and joints. The system also provides multidimensional information about the size, shape, texture and temperature of the objects.

2.3.1. Anatomical basis

Haptic perception begins with the activation of peripheral afferents that provide the initial sensory information about the external world. Eight of the thirteen kind of afferent fibers are responsible for the tactile and haptic input. Four of these provide information about discriminative touch (SA-I, SA-II, FA-I and FA-II), and the other four provide information about body position and movement (muscle spindles types I-II, Golgi tendon organs and joint receptors). These ascending pathways comprise three different stages: First, primary afferents send projections to the dorsal column nuclei (DCN). The projections of the DCN cross the midline at medial lemniscus and synapse onto the ventral posterior lateral (VPL) nucleus of the Thalamus. Then, the Projections from the VPL reach the III and IV layers of the primary somatosensory (SI) and secondary somatosensory (SII) cortices (Hsiao & Yau, 2008).

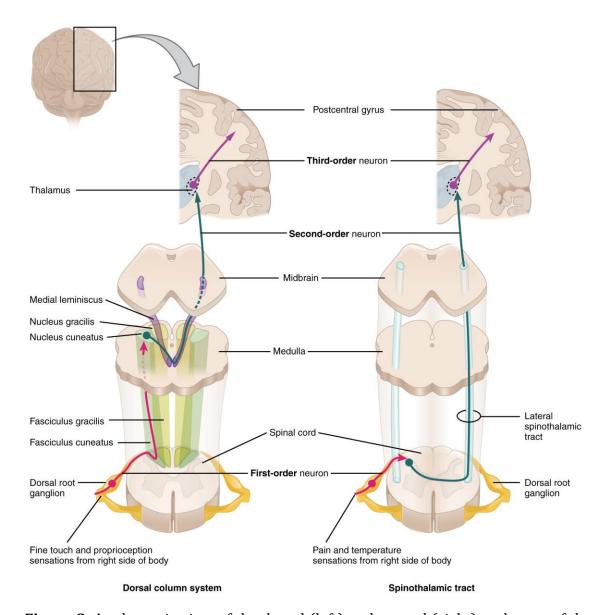


Figure 3. A schematic view of the dorsal (left) and ventral (right) pathways of the somatosensory system responsible for haptic perception and control of movement (By OpenStax College-Anatomy Physiology, Connexions Web http://cnx.org/content/col11496/1.6/, BY Jun 2013., CC3.0, https:// commons.wikimedia.org/w/index.php?curid=30148004)

After entering the SI, the tactile/haptic information is further processed following two cortical pathways that correspond to the "what" and "where" systems described in Section 2.2. The **dorsal** stream transmits the information regarding the location of features and objects to the intraparietal sulcus (IS) and frontal eye fields (FEF), where it interacts with motor areas to guide actions and motor tasks. The **ventral** stream, on the other hand, carries information mainly

about object features and especially surface texture (which is particularly salient in touch) to the parietal opercular cortex (POC) and medial occipital cortex (MOC). Interestingly, the cerebral areas implicated in tactile/haptic processing outside SI in both cortical pathways are also involved in the processing of the corresponding visual information, suggesting that the information from different senses could share the same multisensory representational code (Sathian, 2016).

2.3.2. Neural basis of form and texture perception

There is compelling evidence to suggest that 2D-form and texture perception depend on the afferent SA-I system associated with Merkel complexes. SA-I afferents send to the central nervous system an isomorphic representation of the 2D spatial patterns of the skin. The neural code that is supposed to support 2Dform and texture perception is one based on the spatial variations in firing rate among SA-I afferents (Johnson, Hsiao, & Yoshioka, 2002). Cortically, texture and 2D-form are first processed in the 3b area of the SI cortex. The receptive field structure of this area indicates that representations in this cortical stage are based on the activation of a set of feature detection neurons (similar to primary visual cortex), with an added temporal component that lags the spatial responses and defines an integration period which allows feature integration (Hsiao, Lane, & Fitzgerald, 2002). After this first stage, information is sent to the more complex and less understood neurons of the areas 1 and 2 of the SI cortex. These neurons do not work as point detectors; instead they are thought to represent spatial patterns in a high-order abstract space that involves object representation. In the ventral stream, the signal is sent to the SII cortex where the inputs from the SI, thalamus and ventroposterior inferior nucleus converge. The neurons of this area have large receptive fields that cover much of the contralateral hand and also show of complex spatial patterns and 3D shape. They are also affected by selective attention, supporting the role of the SII cortex in the late high order processing that leads to haptic perception (Gomez-Ramirez, Hysaj, & Niebur, 2016).

A series of studies have investigated the cortical correlates of roughness perception (Kitada et al., 2005). Particularly, Ballesteros, Muñoz, Sebastián, García and Reales (2009) investigated how two tactual stimuli varying in roughness modulated earlier stages of brain activation. The results showed a biphasic N100-P200 deflection that occurred earlier for the smoother than for the rougher texture. The N100 component was related to the activation that occurred at the somatosensory cortex. The P200 was related to the posterior cingulate cortex, indicating that both brain areas participated in the haptic texture perception.

Regarding proprioceptive mechanisms and how they represent body position, far less is known. The proposed mechanism underlying limb positioning and joint angle relies on muscles spindles. Experimental evidence shows that muscle spindle activation leads to altered estimates of joint angles (up to 40°) and can produce limb movement illusions (the Pinocchio effect). In addition, SA-II cutaneous mechanoreceptors also play a role in proprioception, as they could encode joint position due to their sensitiveness to the skin stretch produced during joint movement. Besides the peripheral mechanisms, centrally generated motor signals are also involved in proprioception, as suggested by the limb position judgment errors made by subjects under conditions of muscular fatigue (Hsiao & Yau, 2008).

Finally, the cortical mechanisms responsible for proprioception are still not well understood. What seems clear is that our brain must integrate the information received from peripheral receptors (joint receptors, muscle spindles and

cutaneous mechanoreceptors), along with the brain generated motor commands to generate a representation of the body position and movement in the space (Hsiao & Yau, 2008).

3. Perceptual organization and grouping in the sense of touch

Perceptual organization and grouping phenomena have been investigated exhaustively in visual modality and, to a lesser extent, in audition. However, very few studies explicitly deal with the organizational issues in the tactile modality, and tactile perceptual reviews have largely ignored the topic, even though touch is considered (together with vision and audition) one of the *spatial* senses (Gallace & Spence, 2011).

The first thought about the lack of studies addressing this topic could be that perceptual organization and Gestalt grouping are not so important to understand tactile perception (e.g., Révész, 1953). However, this is not the case, and the absence of published research exploring tactile perceptual organization can be attributed to other reasons that have hindered the progress in this area of research. Particularly, the difficulty associated with the presentation and control of complex tactile displays and the serial nature of tactile information acquisition. Regarding the first difficulty, the development of new tactile systems makes this issue much less problematic (Gallace, Tan, & Spence, 2007). As for the second difficulty, the serial nature of touch is perfectly compatible with the idea of tactile representations not being only the sum of unconnected elements (Gallace & Spence, 2011), as has been demonstrated by Gestalt grouping in audition, where

serial processing is ubiquitous. In addition, the observation that general organizational laws seem to govern perception (suggesting an innate origin of the grouping factors), the similarities found between visual and tactile perceptual information processing (Gallace & Spence, 2008), and the fact that perception is multimodal most of the time can lead us to the conclusion that organizational and grouping phenomena are not exclusive of a particular sensorial modality (Spence, 2012). These findings and developments have led to a renewed interest in the study of perceptual organization and grouping in touch. In the next sections, we will review the evidence addressing the functioning of the perceptual organization in touch, focusing on two main phenomena: figure/ground segregation and perceptual grouping principles.

3.1. Figure/ground segregation

To recognize objects by touch, as in vision, it is necessary to separate them from the background. In the simplest situation, when an object is placed in the hand, it is automatically and physically separated from the background (the hand and the rest of the body). The segregation in this case is provided by the self-awareness of our body, which can be considered the most important feature of figure/ground segregation in touch (Tsakiris, Costantini, & Haggard, 2008). However, the plasticity of our own body representation, that can change in certain conditions (Cardinali et al., 2009), indicates that the figure/ground segregation in touch is not as trivial as it seems. An interesting situation occurs when an object lies among other objects (haptic recognition) and the objective of the tactile system is to segregate the object from the background to grab it and use it. Even though the studies in this area have never linked their results with organizational and grouping laws, they show that recognition performance varies depending on

the conditions of stimulus presentation, such as the time allowed to explore, and the nature of the material, which is better for real objects. The most interesting studies in figure/ground segregation are those that investigate the ability to discriminate raised line patterns from distractors in visually impaired and blindfolded participants (e.g., Heller, Wilson, Steffen, Yoneyama, & Brackett, 2003). The results from this kind of studies showed that both, blind and sighted participants can segregate a tactile pattern from the background even though the visually impaired cannot transform the tactile input into a visual code, suggesting a tactile figure/ground segregation process per se.

3.2. Grouping principles

We will discuss various grouping principles and their application to the tactile modality, as well as the similarities and differences between the results obtained in touch and those that investigate the same issues in the visual modality.

One of the first grouping phenomena that have been studied in the tactile modality, at least indirectly, is **perceptual completion**, which is thought to depend on the Gestalt principle of **closure**. Completion is necessary for object recognition in touch, as we need to complete the gaps between the fingers to obtain a complete representation of the object. The majority of the studies are based on the object recognition itself and do not mention the possible effect of completion (e.g., Woods, Moore, & Newell, 2008). The first study addressing the topic was conducted by Kitagawa, Igarashi, and Kashino (2009). They reported that when a vibrotactile target contained small temporal gaps and those gaps where filled with a vibrotactile noise, the target vibration was perceived as continuous. In addition, the participants were unable to distinguish this illusory continuity from a real continuous vibrotactile target. This result suggests that

participants are capable of completing the temporal gaps between stimuli. Moreover, it would constitute a form of modal completion, as participants feel the presence of a stimulus with the same characteristics as the real one. Indirect support for tactile closure comes from the study conducted by Overvliet, Smeets, and Brenner (2008). In the experiment, participants had to find the interruption of a straight line under one of their fingertips. The participants had difficulties in finding a line among distractors and the gap itself. The authors linked the effect to the participants "filling in" the gap when the line endings where close. Finally, studies of tactile-vision substitution with visually impaired people also support completion presence in the tactile modality. These devices transform visual images into a matrix of tactile transducers placed on the back of the participants. The participants were able to "translate" visual objects into tactile images and perceive complete and uniform images (Collins, 1970).

The functioning of the Gestalt principle of **continuation** has also been investigated in the tactile modality by Chang, Nesbitt, and Wilkins (2007), who performed the first study directly investigating this Gestalt principle in touch. They presented several visual and tactile layouts and found that participants interpreted both, the visual and the haptically explored displays, as if they were continuous lines and forms, suggesting that both sensor modalities completed the missing information in the same manner.

Finally, the grouping principles of **proximity** and **similarity** have been investigated in the tactile modality in a study conducted by Chang, Nesbitt, and Wilkins (2007b). The participants explored haptic stimuli composed of 7-16 elements that differed in surface texture or space between items and verbally reported the number of groups perceived. The findings showed that participants

grouped elements by surface texture when the distance between elements was constant. However, proximity determined the number of groups when the distance between elements was varied. A different approach to investigating the applicability of proximity and similarity grouping principles in touch has been to study their influence in the performance of different tasks. In this vein, grouping by spatial proximity has proven to facilitate haptic search (Overvliet, Krampe, & Wagemans, 2012), contour detection (Overvliet, Krampe, & Wagemans, 2013), numerosity perception (Verlaers, Wagemans, & Overvliet, 2015) and haptic enumeration (Overvliet & Plaisier, 2016). On the other hand, grouping by similarity (specially texture similarity) has also proven its influence on haptic search, especially when the difficulty of the task increases and more cognitive resources are needed (Van Aarsen & Overvliet, 2016).

Overall, these results support the hypothesis that at least some grouping principles (proximity, similarity, closure or continuation) and other perceptual organization processes (figure/ground segregation) are applicable to the tactile modality, following similar rules to those of the visual modality.

CHAPTER 4: OBJECTIVES AND HYPOTHESES

1. Objectives

This thesis had three primary goals. The first goal was to analyze the time course and dominance dynamics of grouping principles in the haptic modality. We focused on the analysis of the grouping principles of spatial proximity and texture similarity that are known to operate in touch (see Section 3.2). To this end, we assumed the classic rules of processing dominance in the psychophysical literature (Navon, 1977; Ward, 1983). According to these rules, a grouping cue will dominate the perceived organization if: 1) it produces faster and/or more accurate responses; 2) it is less interfered by the competitive presence of another cue (i.e. when each grouping cue favors opposite perceptual organizations); and 3) it improves the responses to another cue when both grouping cues are presented in cooperation, (i.e. when both cues contribute to strengthen the same perceptual organization). To achieve this objective, in Experiments 1 and 2 (see Chapters 5 and 6), we employed a haptic speeded orientation task which gave us information about the time course of both grouping principles acting alone, thus informing us about the first of the 3 dominance criteria. In addition, in Experiments 4, 5 and 6 (see Chapters 7 and 8), we employed two different psychophysical methods (directed and non-directed attention to the grouping task) in which grouping principles appeared acting alone or conjoined in cooperation or competition within the same stimulus. This set of experiments allowed us to obtain information about the second and third criteria of perceptual dominance, as well as further evidence on the first criterion.

The **second** goal of this investigation was to study the interactions between grouping principles in the haptic modality and their compatibility with an additive model of grouping effects. We based our predictions about additivity on the model

proposed by Kubovy and van den Berg (2008), who stated that additive effects can be inferred if: 1) the grouping strength of the cooperation condition is greater than the grouping strength of the grouping principles acting alone; and 2) the grouping strength of both principles combined in competition is weaker than the strength of the grouping principles acting alone. For this purpose, in Experiment 3 (see Chapter 7), we employed a phenomenological task in which participants had to rate the perceived subjective strength of grouping in three grouping conditions (acting-alone, cooperative, and competitive). This task also allowed us to ensure that the perceived phenomenological strength of proximity and similarity was equated. The psychophysical tasks developed for Experiments 4, 5 and 6 (see Chapters 7 and 8) also provided convergent evidence on the additivity of grouping effects through objective tasks in which correct/incorrect responses were objectively defined.

Finally, the **third** objective was to investigate the neurophysiological correlates (oscillatory brain activity) of haptic grouping by proximity and similarity when both principles act in isolation or conjoined within the same stimulus. In Experiment 2, we focused on the spectral power changes of alpha and beta bands over sensorimotor and parietal regions (μ sensorimotor rhythm) and occipital areas, during an orientation detection task in which grouping principles appeared always in isolation. In Experiments 5 and 6, in contrast, we analyzed alpha and beta band oscillatory activity in a task in which grouping principles appeared both in isolation and conjoined in a cooperative or competitive manner.

2. Hypotheses

According to the objectives of the present thesis, we can formulate three main experimental hypotheses:

- First, given the results from previous studies on the time course and dominance dynamics of proximity and similarity grouping principles in the visual modality (Han, 2004; Han et al., 2002, 2001; Mao, Han, Guo, & Jiang, 2004), and the similarities found in the way in which individuals organize the perceptual scene in both tactile and visual modalities (Chang et al., 2007b), we hypothesize that proximity will dominate haptic grouping. This dominance will be reflected in: 1) faster and more accurate responses in stimuli grouped by proximity compared to those grouped by similarity (Experiments 1, 2, 4, 5 and 6); 2) greater interference/facilitation effects when proximity acts as the interfering feature, relative to conditions in which similarity is the interfering feature (Experiments 4, 5 and 6).
- Second, we hypothesize that the interactive effects of grouping principles will be compatible with an additive model (Kubovy & van den Berg, 2008), as measured by subjective phenomenological ratings (Experiment 3) and objective psychophysical measures (RTs and accuracy) (Experiments 4, 5 and 6).
- Third, we expect a bilateral activation of a network of sensorimotor and parietal areas, reflected in the spectral power reduction (event related desynchronization or ERD) of alpha and beta bands over ipsi and contralateral cortices. We also expect increased activity within this network in similarity relative to proximity conditions, especially in sensory integration areas, due to

the need to integrate the sparse texture information into a unified percept (Experiment 2). In addition, we hypothesize that conditions in which both grouping principles compete will lead to increased activity (greater ERD) in frontal and parietal regions related to conflict processing and resolution, especially when proximity is the interfering cue (Experiments 5 and 6) in accordance with the first hypothesis.

CHAPTER 5: TIME
COURSE OF
GROUPING BY
PROXIMITY AND
SIMILARITY IN A
HAPTIC SPEEDED
ORIENTATION TASK

Time course of grouping by proximity and similarity in a haptic speeded orientation

Antonio Prieto, Julia Mayas, and Soledad Ballesteros

{antonioprieto@psi.uned.es, jmayas@psi.uned.es, mballesteros@psi.uned.es}

Departamento de Psicología Básica II, Studies on Aging and

Neurodegenerative Diseases Research Group

Prieto, A., Mayas, J., & Ballesteros, S. (2014). Time course of grouping by proximity and similarity in a haptic speeded orientation task. LNCS, Haptics: Neuroscience, Devices, Modeling, and Applications; Vol. 8618, Part I, pp. 379-385.

Abstract

Behavioral and neurophysiological findings in vision suggest that grouping by proximity occurs earlier than grouping by similarity. The present study investigated in the haptic modality whether proximity is an earlier/faster grouping principle than texture similarity. In this study, we compared responses to stimuli grouped by proximity with that grouped by similarity (surface texture) using a speeded orientation detection task performed on a novel haptic device. The apparatus was interfaced with a computer to allow controlled stimulus presentation and accurate registration of the responses. Two were the main results of the experiment: (1) response times for stimulus patterns grouped by proximity were faster compared to those patterns grouped by similarity; and (2) in those patterns grouped by proximity, vertical symmetric patterns were classified faster than horizontal symmetric patterns. We conclude that the Gestalt principles of proximity and similarity apply to the haptic modality. As in vision, grouping by proximity is faster than grouping by similarity, especially when symmetric grouped patterns are oriented vertically in line with the body midline axis.

Keywords: Bilateral symmetry \cdot Gestalt \cdot Grouping principles \cdot Haptic perception \cdot Perceptual grouping \cdot Proximity \cdot Similarity

1. Introduction

Since the early 20th century, when the Gestalt Psychology formulated the perceptual grouping principles, the research efforts in the field focused primarily in vision and audition (Wagemans, Elder, et al., 2012). Little research was directed to investigate whether these perceptual grouping principles apply also to touch. The main reasons were the early claims on the lack of applicability of the Gestalt principles to touch, and (Scholtz, 1957) problems related to the presentation of the stimuli and the registration of the responses. Even recent reviews on tactile perception have treated the topic very scarcely (Gallace & Spence, 2011). However, in recent years, there has been a renewed interest on the subject (Chang et al., 2007b, 2007a, Overvliet et al., 2012, 2013). Specifically, Chang et al. (2007b) investigated the applicability of proximity and texture similarity grouping to the haptic modality. Their results indicated that participants group both, visual and tactile patterns in a similar way and that proximity was a more powerful grouping principle than similarity. More recently, Overvliet et al. (2012, 2013) demonstrated that both, proximity and similarity influence haptic search and contour detection. However, these studies did not address the question of which of these two principles occur earlier in the processing stream. In vision, behavioral and neurophysiological evidence suggests that grouping by proximity is faster than grouping by similarity (Han, 2004; Han et al., 2002).

The aims of the current study were twofold: (1) to examine whether these two principles have time courses in touch similar to those previously reported in vision, and (2) to investigate the influence of the orientation (vertical/horizontal with respect to the haptic explorer) and total size of the pattern (square or

rectangular) of the grouped elements on the speed of processing. To achieve these aims, an orientation detection task similar to the one used in vision by Han (Han, 2004) was adapted to touch. To present the stimuli and register the responses, we used a specifically designed haptic apparatus (MonHap) based on one used previously to investigate the lateralization in haptic processing(Fagot, Arnaud, Chlambretto, & Fayolle, 1992).

Given that the proximity and similarity grouping principles seem to operate similarly in vision and touch, it might be hypothesized that orientation will be detected faster in stimulus patterns grouped by proximity compared to those grouped by similarity. Additionally, we also hypothesized that bilateral symmetric patterns grouped by proximity in the vertical plane will be detected faster than in the horizontal plane due to the advantage of the vertical axis in the detection of bilateral symmetry (Ballesteros, Manga, & Reales, 1997; Ballesteros, Millar, & Reales, 1998; Ballesteros & Reales, 2004; Palmer & Hemenway, 1978).

2. Method

2.1 Participants

Seventeen (15 female, 2 male) volunteer undergraduate students at the Universidad Nacional de Educación a Distancia participated in the study. Their mean age was 34 years (SD = 10.06; range 20–49). All participants were right-handed, had normal visual and tactile performance and were naïve to the purpose of the experiment. Informed consent was obtained from each participant. The study was approved by the UNED Ethics Committee.

2.2 Stimuli and Apparatus

The stimuli consisted of 24 touch-sensitive cylinders of approximately 13 mm x 15 mm x 15 mm specifically designed for the experiment. Sixteen cylinders had a metallic smooth texture and the remaining had a rough texture created by covering the cylinder surface with sandpaper (n° 4). The stimuli were combined in groups of 12 or 16 to form a total of 12 Gestalt grouped vertically/horizontally oriented patterns that were presented in a different random order to each participant. Horizontal stimuli were those that, by means of the grouping principle used (proximity or texture similarity), formed two rows of elements perpendicular to the mid-transverse plane of the participant's body. Vertical stimuli were those that formed two rows of elements parallel to the mid- transverse plane of the participant's body (see Figure 1).

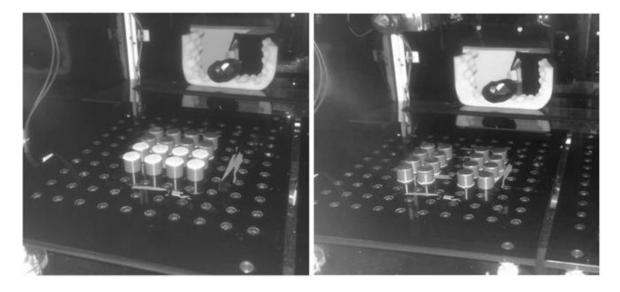


Figure 1. Left: A horizontally oriented pattern grouped by texture-similarity. Right: A vertically oriented pattern grouped by proximity.

The MonHap haptic devise was used for stimulus presentation and data collection. The device consisted of an opaque box with two apertures to introduce

the hands and two platforms containing an array of 10×10 small holes where the cylinders were plugged in to create the desired configuration. The haptic devise was interfaced with a computer to control stimulus presentation and to record exploration times and accuracy.

2.3 Design and Procedure

The task consisted of detecting the vertical or horizontal orientation of patterns formed by small cylinders. On each trial, the participant explored the grouped pattern with his/her dominant hand and decided as fast and accurately as possible whether the pattern was oriented vertically or horizontally by pressing one of two foot-pedals. Pedals were counterbalanced across participants. The stimulus patterns were constructed by grouping the small cylinders either by proximity or by similarity to form two rows of grouped elements, which were oriented vertically or horizontally relative to the participant's body midline. Along with the *grouping type* (proximity, texture similarity) and *orientation* (vertical, horizontal), the *total size* of the pattern was also manipulated $(3 \times 4, 4 \times 4)$ resulting in a factorial $2 \times 2 \times 2$ within-subjects design. Participants performed two blocks of 56 trials including six practice trails that were not included in the data analysis, with a 5 min resting interval between each block.

The participant seated comfortably in front of the apparatus introduced his/her dominant hand through the aperture and explore the pattern located at the presentation platform. A green LED light located in front of the participant signaled the start of the trial. Participants were instructed to place their hand palm over the stimulus after the onset of the green light, to explore the pattern freely and to press one pedal for vertical patterns and the other for horizontal ones. Exploration

time was recorded from the initial contact of the hand with the stimuli until response. Accuracy was also recorded.

3. Results

The Shapiro-Wilk test for normality of the RT data showed that 2 of the 8 conditions differed significantly from a normal distribution. In order to fit ANOVA assumptions RT data was Log-transformed. After the transformation, all conditions fitted the normal distribution (Shapiro-Wilk test, all p > .05). A 2 (grouping type: proximity, texture- similarity) × 2 (*orientation*: horizontal, vertical) × 2 (*total size*: 3 × 4, 4 × 4) repeated measures ANOVA was conducted on Log-RTs for correct responses. Multiple comparisons were Bonferroni corrected. RTs above and below 2.5 times the standard deviation of each participant were removed from the analysis. Overall, 2.25 trials were removed from each participant (range 0-4) which represent 2.14 % of valid trials. One participant was excluded from the analysis due to the large number of errors (78.6 %). The ANOVA showed that the main effect of grouping type was statically significant [F(1, 15) = 28.92; p < .001; $\eta 2p = .658$]. Participants were faster detecting the orientation of patterns grouped by proximity (1504 ms) relative to those grouped by texture similarity (1960 ms). The main effect of *orientation* was also significant $[F(1,15) = 15.49; p = .001; \eta 2p = .001]$.508], showing that participants were faster detecting the orientation of vertically oriented patterns (1642 ms) relative to horizontally oriented patterns (1822 ms). Finally, the main effect of *total size* also reached statistical significance [F(1, 15)] = 15.09; p = .001; $\eta 2p = .502$]. Participants were faster with square (4 × 4) patterns (1675 ms) than with rectangular (3×4) patterns (1790 ms), in which orientation of the entire pattern was always contrary to the orientation of the grouped stimuli. Furthermore, the significant *grouping type* x *orientation* interaction [F (1, 15) = 14.54; p < .001; $\eta 2p = .492$] qualifies part of the main effects discussed above. *Post hoc* contrasts revealed that participants were faster identifying vertically oriented stimuli (1354 ms vs. 1654 ms) but this was only true for stimuli grouped by proximity [F (1, 15) = 19.31; p = .001; $\eta 2p = .563$]. No other interactions reached statistical significance (see Figure 2 left).

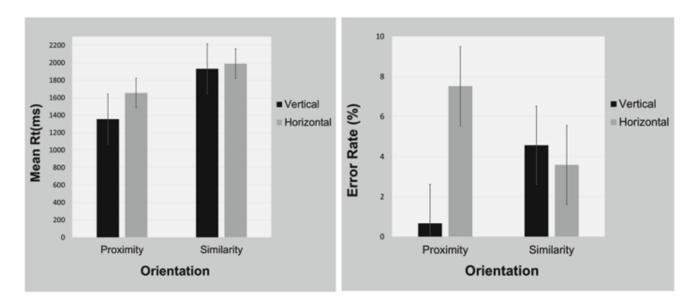


Figure 2. Left: mean reaction times for vertical and horizontal patterns grouped by proximity and by similarity. Right: percentage of errors as a function of pattern orientation and type of grouping. Error bars represent the standard error of the mean.

Unlike RT data in which violations of ANOVA assumptions were minor, the Shapiro-Wilk test for normality of the accuracy data showed that all conditions differed significantly from a normal distribution (all 8 conditions p < .05), so we decided to carry out nonparametric tests on the accuracy data. We first tested which mean error rates were significantly different from 0, to avoid testing ceiling effects. In all conditions except vertical/proximity-grouped stimuli (0.67 %; $p = \frac{1}{2}$)

.083; Wilcoxon signed rank test), mean error rates were significantly different from 0 (all p < .05; Wilcoxon signed rank test). Participants made significantly more errors (Z = 2.17, p < .05; Wilcoxon signed rank test) in detecting horizontal patterns (5,86 %) relative to vertical ones (2.62 %). Furthermore, participants committed more errors (Z = 3.22, p < .05; Wilcoxon signed rank test) in horizontal/proximity-grouped trials (8.12 %) relative to vertical/proximity-grouped trials (0.67 %). No other effects reached statistical significance (see Figure 2 right).

4. Discussion

The present study investigated the time course of the proximity and similarity grouping principles in touch. Our results showed that as in vision, participants were faster with stimuli grouped by proximity relative to those grouped by texture similarity. This may be related to the type of processing. In vision, grouping by proximity has been related to fast global processing and low spatial frequencies analysis while similarity grouping may be related to local processing and high spatial frequencies analysis (Wagemans, Elder, et al., 2012). The same seems to happen in active touch in which the spatial relationship between the elements of the haptic pattern (spatial proximity) would be a more global feature than the specific properties of each element (texture), thus leading to a faster identification of patterns grouped by proximity. The interaction between *orientation* and *grouping type* suggests that patterns oriented vertically are identified faster and more accurately than those oriented horizontally, but only when the stimuli were grouped by proximity. This effect may be related to the differences in symmetry of patterns grouped by proximity and those grouped by similarity. In this case,

stimuli grouped by proximity have bilateral/mirror symmetry, in which half of the pattern is a mirror reflection of the other half (Weyl, 1989). Visual literature indicates that bilateral symmetry is the most salient, followed by horizontal and oblique orientations (Wagemans, 1995). Our results agree with those obtained in vision that showed faster RTs and more accurate responses for vertical proximitygrouped patterns than for horizontal ones. Moreover, the findings are also consistent with research in symmetry discrimination by touch (Ballesteros et al., 1997, 1998; Ballesteros & Reales, 2004) in which bilaterally symmetric objects along the body midline axis (same symmetry axis as our vertical stimuli) showed an advantage over other axes of symmetry. An alternative explanation for the faster RTs obtained in proximity grouping conditions could be related to the use of different exploration strategies depending on the type of grouping, that is, when stimuli were grouped by proximity a marker of the array orientation was available at the center of the stimulus. In this case, exploring the stimulus midline would result in faster responses relative to similarity-grouped stimuli that require a more detailed exploration. However, this alternative explanation is also compatible with the global/local processing hypothesis. In fact, to explore the stimulus midline could be considered a more global exploration strategy, effective only for those stimuli grouped by proximity. In contrast, stimuli grouped by similarity may require a more detailed exploration of the local features of the stimulus to achieve a complete representation of the pattern.

To conclude, our work replicates in the haptic modality two well-known findings in vision: (1) faster RTs for stimuli grouped by proximity relative to those grouped by similarity; and (2) faster and more accurate identification of symmetric

patterns oriented vertically relative to those oriented horizontally thus suggesting a body midline advantage found in previous haptic symmetry detection studies.

CHAPTER 6: AI PHA AND BETA BAND CORRELATES OF HAPTIC PERCEPTUAL **GROUPING: RESULTS** FROM AN ORIFNTATION DETECTION TASK

Alpha and beta band correlates of haptic perceptual grouping: results from an orientation detection task

Antonio Prieto^{1*}, Julia Mayas¹ and Soledad Ballesteros¹

¹ Studies on Aging and Neurodegenerative Diseases Research Group,

Departamento de Psicología Básica II, Facultad de Psicología, Universidad Nacional

de Educación a Distancia, Madrid, España.

Prieto, A., Mayas, J. & Ballesteros, S. (2018). Alpha and beta band correlates of haptic perceptual grouping: Results from an orientation detection task. PLOS ONE 13(7): e0201194. https://doi.org/10.1371/journal.pone.0201194

Abstract

Behavioral and neurophysiological findings in vision suggest that perceptual grouping is not a unitary process and that different grouping principles have different processing requirements and neural correlates. The present study aims to examine whether the same occurs in the haptic modality using two grouping principles widely studied in vision, spatial proximity and texture similarity. We analyzed behavioral responses (accuracy and response times) and conducted an independent component analysis of brain oscillations in alpha and beta bands for haptic stimuli grouped by spatial proximity and texture similarity, using a speeded orientation detection task performed on a novel haptic device (MonHap). Behavioral results showed faster response times for patterns grouped by spatial proximity relative to texture similarity. Independent component clustering analysis revealed the activation of a bilateral network of sensorimotor and parietal areas while performing the task. We conclude that, as occurs in visual perception, grouping the elements of the haptic scene by means of their spatial proximity is faster than forming the same objects by means of texture similarity. In addition, haptic grouping seems to involve the activation of a network of widely distributed bilateral sensorimotor and parietal areas as reflected by the consistent event-related desynchronization found in alpha and beta bands.

1. Introduction

Perceptual grouping refers to "the fact that observers perceive some elements of the visual field as going together more strongly than others" (Wagemans, Elder, et al., 2012). Research efforts addressing the specific principles that determine how perceptual grouping occurs and the mechanisms that govern its operation have focused primarily on vision and audition, where grouping principles have been relatively well established (Wagemans, Elder, et al., 2012; Wagemans, Feldman, et al., 2012). To date, however, little research has been conducted to investigate whether these perceptual grouping principles also apply to the sense of touch. There are, at least, three main reasons: First, the early claims about the lack of applicability of the Gestalt principles to touch (Révész, 1953); second, the serial nature of tactile exploration, and third, difficulties related to the controlled presentation of the stimuli and response registration. Even reviews of tactile perception have scarcely touched on the topic (Grunwald, 2008; Lederman & Klatzky, 2009). However, in the last decade, there has been renewed interest in this topic (Gallace & Spence, 2011), guided both by the theoretical interest in knowing the shared and/or specific mechanisms behind grouping in different sensory modalities, and the potential practical applications that a better knowledge of how the tactile perceptual scene is organized into meaningful objects may have in several areas. Among these areas are the design of visuo-tactile/haptic displays and interfaces, and the development of tactile resources and substitution devices for visually impaired people.

Specifically, Chang, Nesbitt and Wilkins (2007b) used visual and haptic layouts composed of 7 to 16 squares that vary in proximity and similarity (color/texture)

and asked their participants to indicate the number of groups and the reason they based their response. The researchers found that participants grouped visual and tactile patterns in a similar way. The same occurred when participants had to group the elements using the Gestalt principle of continuation (Chang et al., 2007a). More recently, Overvliet, Krampe and Wagemans (2012, 2013) conducted two studies in which participants either explored haptic random dot displays (contour detection) or columns composed of vertical and horizontal lines (haptic search). The authors demonstrated that proximity and similarity grouping principles influence haptic contour detection and haptic search respectively. Finally, Verlaers, Wagemans and Overvliet (2015) and Overvliet and Plaisier (2016), using haptic enumeration tasks in which participants were asked to count tangible dots while moving their finger pads over a tactile display, showed that both proximity and configural grouping cues can speed up haptic enumeration. These convergent results suggest the existence of similar underlying mechanisms in visual and haptic perceptual grouping. However, these similarities should be taken with caution, given the fundamental differences in how the sensory information is acquired in each sensory modality. Particularly, in vision the information processing is largely parallel. In contrast, the acquisition of sensory information during haptic exploration is sequential (which involves active movements not totally under experimental control) and may involve other cognitive processes that are not present in visual tasks (e.g., the activation of working memory processes to keep haptic information available during the exploration).

A fundamental question is whether perceptual grouping is a unitary process that underlies all grouping principles (Ruth Kimchi & Razpurker-Apfeld, 2004).

Traditional views assume that grouping is an early single process along the cognitive stream, consisting of combining similar types of tokens into larger ones, and to construct the boundaries between different sets, a process that provides the units which other perceptual processes will use as input (Neisser, 1967; Treisman, 1982). Nonetheless, the empirical evidence challenges the notion that grouping is a simple and unitary phenomenon. On this line, findings indicate that perceptual grouping is formed by, at least two different processes: 1) a unit formation and clustering process responsible for determining which elements belong together and the segregation from other elements, and 2) a shape formation, or configuring process, involved in the global appearance of the grouped elements depending on their interrelations. This processes would take place at different processing stages, and might have different cognitive requirements (Ruth Kimchi & Razpurker-Apfeld, 2004; Razpurker-Apfeld & Kimchi, 2007). This view implies not only that different grouping principles implicate different cognitive resources and neurological correlates (Nikolaev, Gepshtein, Kubovy, & Van Leeuwen, 2008), but also that the time needed to group the elements of the perceptual scene will be different depending on the features (spatial arrangement, shape, texture) in which the grouping process is based.

The latter question has been specifically addressed in the visual modality by comparing proximity and similarity grouping principles. Results suggest that behavioral responses to stimuli grouped by proximity are faster than to those grouped by similarity, and that electrophysiological substrates and processing requirements would be different in the two principles (Han, 2004). More specifically, Han Ding and Song (2002) as well as Han, Song, Ding, Yund and Woods (2001) found that the perception of stimuli was faster and more accurate

when they were grouped by spatial proximity than by color/shape similarity, and that both principles followed distinct neural pathways (dorsal/ventral stream, respectively). Moreover, according to Mao, Han, Guo and Jiang (2004), the faster behavioral responses to stimuli grouped by proximity in vision are due to the fact that proximity grouping modulates activity in the primary visual cortex early (60-90 ms), whereas similarity grouping does not. These results suggest that the formation of objects based on the spatial relationships of their constituent elements is faster than that based on the characteristics that are common to those elements.

Only a few visual studies have addressed the neural basis of perceptual grouping from the time frequency perspective, and their methodologies and results are mixed. For example, Volberg, Wutz and Greenlee (2013) found increased beta-band power over occipito-parietal sites in a contour detection task when the participants were able to perceive the contour. Also, Aissani, Martinerie, Yahia-Cherif, Paradis, and Lorenceau (2014) reported increased beta-band activity in centro-parietal sites when stimuli where perceived as a whole in a form/motion perceptual integration task. By contrast, Zaretskaya and Bartels (2015) found decreased beta-band power over posterior parietal sites associated with global Gestalt perception and perceptual grouping. This contrasting pattern of results could be explained by the distinction between local and global processing. For example, Romei, Driver, Schyns, and Thut (2011) found that bursts of right-parietal Transcranial magnetic stimulation (TMS) at beta and theta frequency benefited local and global processing respectively. Thus, the increased beta power in the first two studies could indicate the existence of more local processing requirements.

Grouping studies in the haptic modality have focused mainly on the behavioral study of the applicability of grouping principles to touch and their influence over other cognitive processes (Chang et al., 2007b, 2007a; Overvliet & Sayim, 2016; Overvliet et al., 2012, 2013; Overvliet & Plaisier, 2016; Verlaers et al., 2015). However, there is no direct empirical evidence that accounts for both the behavioral and the neural correlates of perceptual grouping in touch (Gallace & Spence, 2011), but see Blankenburg, Ruff, Deichmann, Rees and Driver (2006) for an indirect approximation to the study of the neural correlates of haptic grouping.

In the present study, we investigated the behavioral (RTs and accuracy) and electrophysiological correlates (time/frequency oscillatory brain activity) of spatial proximity and texture similarity for stimuli presented to touch without vision. We focused on transient event-related spectral perturbations (ERSP) of alpha and beta bands over sensorimotor and parietal regions, a measure of the event-related shifts in the power spectrum during the task period. The power changes within these frequency bands constitute the predominant activity of the so-called µ sensorimotor rhythms (SMR) (Vukelić et al., 2014). Furthermore, given that previous studies have shown the involvement of visual areas in haptic processing (Sathian, 2005; Snow, Strother, & Humphreys, 2014), we also focused on alpha band activity within the occipital cortex as an indicator of the activity of visual areas when exploring stimuli by touch. To avoid the confound derived from the mixed EEG signals recorded from the scalp (which include contributions from different brain sources), we employed independent component analysis (ICA) and clustering methods (Bell & Sejnowski, 1995) instead of the raw data from scalp electrodes to decompose the EEG recorded signal into the maximally temporally independent signals available in the data channels (also called independent

components -ICs). Then, we performed the brain activity analyses on the resultant ICs. This separation and identification of independent brain sources is essential to characterize the neuropsychological origins of the brain processes, and to relate a specific task with the activity and topography of those brain sources (Jung et al., 2001). We used a touch-adapted speeded orientation detection task similar to the one used in vision by Han (2004). To present the haptic stimuli and record the participants' responses, we used a specifically designed haptic device (MonHap) adapted from an apparatus originally designed to investigate lateralization in haptic processing in monkeys (Fagot et al., 1992). This apparatus enabled us to control the presentation of the haptic stimuli and to record EEG activity.

The aims of the current study were twofold: (1) To examine the behavioral differences in speed and accuracy of these two grouping principles in the haptic modality; and (2) to investigate the brain oscillatory activity of grouping by proximity and grouping by similarity for stimuli presented by touch.

Given that previous studies (Chang et al., 2007b, 2007a, Overvliet et al., 2012, 2013; Verlaers et al., 2015) have shown that proximity and similarity grouping principles seem to operate similarly in vision and touch, we hypothesized that orientation would be detected faster and more accurately in patterns grouped by proximity compared to those grouped by similarity.

Regarding IC-cluster analysis of brain oscillations (ERSP), we expected the recruitment of a large bilateral sensorimotor network, reflected in the power reduction (event-related desynchronization or ERD) of alpha and beta bands over contra- and ipsi-lateral sensorimotor and parietal cortices. In addition, we hypothesized that activity within this network would increase in the grouping by similarity condition relative to proximity grouping, especially in sensory

integration areas, due to the need to compute two different textures and to integrate this information into a unified percept. As mentioned above, previous studies have shown the contribution of visual areas in haptic processing, especially in object recognition (Amedi, Malach, Hendler, Peled, & Zohary, 2001; Sathian, 2005; Snow et al., 2014), so our aim was also to investigate the involvement of occipital visual areas in haptic perceptual grouping.

2. Method

2.1. Participants

Fifteen (11 females) volunteer students at the Universidad Nacional de Educación a Distancia (UNED) participated in the study. Their mean age was 34 years (SD = 10.06; range 20-49). All participants reported being right-handed, had normal tactile perception and were naïve to the purpose of the experiment. They signed an informed consent form for participation in the study, which was approved by the Ethical Committee of the UNED. The experiment was conducted in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki as revised in October 2008.

2.2. Apparatus and stimuli

The *MonHap* haptic device was used for stimulus presentation and data collection. The device consists of an electromagnetically shielded (to avoid possible artifacts) opaque box with two apertures to introduce the hands and two platforms containing an array of 10 x 10 small holes in which the cylinders were plugged to create the desired configuration. The haptic device was interfaced with two computers. The first controlled the stimulus presentation and recorded exploration times and accuracy. The second recorded the EEG data.

The stimuli consisted of 24 touch-sensitive cylinders measuring approximately 13mm (height) x 15mm (diameter) each, specifically designed for the experiment. Sixteen cylinders had a smooth metallic texture and the remaining had a rough texture created by covering the cylinder surface with sandpaper (see Fig 1a). The stimuli were arranged in patterns of 12 (4 x 3) or 16 (4 x 4) cylinders to form 12 different Gestalt grouped patterns oriented vertically/horizontally, that were matched in number in both grouping conditions (see Fig 1b). All haptic patterns were confined within a 5 x 5 (95 mm x 95 mm total exploration area) square matrix (a sub-matrix of the 10 x 10 array of the *MonHap* device). This arrangement ensured that the haptic exploration area was the same in all the experimental conditions. In the texture-similarity condition (Fig. 1b upper row), the grey circles represent the rough textured cylinders, while the black circles represent the smooth textured cylinders. Thus, in the similarity condition, the two orientations were defined by the different textures that compound the haptic pattern (half rough and the other half smooth), while the distance between the different elements remain constant. On the contrary, in the proximity condition (Fig. 1b) bottom row), all the cylinders had the same texture (smooth in 50% of the proximity trials and rough in the other 50% of the trials), so participants cannot rely on texture differences to identify the orientation of the global pattern, and the orientation of the pattern was defined by the different spatial distance between the elements. Horizontal stimuli were those that, according to the grouping principle used (proximity or texture similarity), formed two rows of elements perpendicular to the mid-sagittal plane of the participant's body (see Fig 1b, right). Vertical stimuli were those that formed two rows of elements parallel to the mid-sagittal plane of the participant's body (see Fig 1b, left). In the similarity conditions, the

gap between each single element was fixed at 6 mm (see Fig 1b, upper row), whereas in the proximity condition the distance between each element was 6 and 25 mm for close and far elements respectively (see Fig 1b, bottom row).

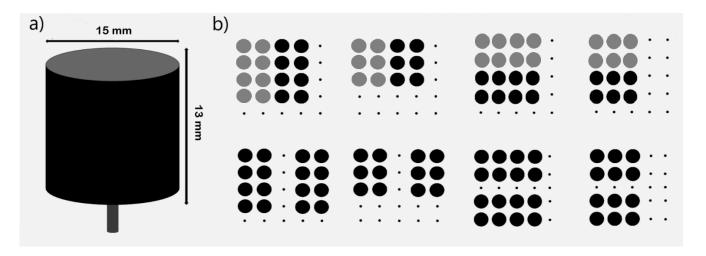


Figure 1. Individual stimuli and patterns used in the orientation detection task

(A) An overview of the individual cylinders used to form the different haptic patterns. (B) Stimulus configurations used in the orientation detection task. The top and bottom rows of Fig 1b show the patterns used for similarity and proximity conditions respectively. The left and right side of Fig 1b shows vertical and horizontal stimuli respectively. In similarity condition (top row), the grey and black circles represent the rough and smooth textures employed for texture-similarity grouping

The experimental room was shielded to avoid electromagnetic artifacts from the outside. Lighting and temperature conditions were kept constant for all participants.

2.3. Procedure

Participants were seated in an armchair facing the front of the MonHap at approximately 30 cm, with the midline of the body aligned with the center of the apparatus. After placing the EEG cap and preparing the electrodes, the experimenter indicated the participants to introduce their right (dominant) hand through the aperture located on the right side of the apparatus (and also located to

the right relative to the body mid-line) and to become familiar with the presentation platform where the stimuli would be presented. To avoid muscular artifacts produced by head, body and arm movements, participants were encouraged to face forward during the experiment, to avoid head movements and maintain eye fixation and to support their backs on the seat and rest their forearm and the edge of their hand on the side of the presentation platform. They were also asked not to touch the stimuli before the start of a trial. Once the participants where comfortably seated, the experimenter gave detailed instructions to the participants about the task. The task consisted of detecting the orientation of patterns formed by means of spatial proximity (where orientation was determined by sets of elements that were spatially close relative to the others) and texture similarity (where orientation was determined by sets of elements with the same texture) grouping principles. Trials with "vertical" orientation were defined as those whose orientation was parallel to the mid-sagittal plane of the body. Trials with "horizontal" orientation were defined as those whose orientation were perpendicular to the mid-sagittal plane of the body. The patterns themselves, were presented in line with the transverse plane of the body (horizontal plane relative to the floor). The experimenter instructed the participants to decide on each trial whether the patterns were oriented vertically or horizontally relative to their body midline, according to the definitions given above, and execute the response as fast as possible but trying to avoid errors. Each trial began with the computer program randomly generating the next configuration and displaying it on a computer screen only visible for the experimenter. The experimenter then arranged the pattern generated, by plugging each individual cylinder in the correct position into the MonHap. Once the stimulus setup was completed, the experimenter guided the

hand of the participant to a predesignated start position within the presentation platform, to ensure that all participants began the haptic exploration in the same conditions. Participants waited in the start position with the edge of their hand placed on the right side of the pattern (without touching it), until a green led light placed in front of the participant signaled the start of the trial. The participants, then, placed the hand over the haptic pattern and used their index, middle, ring and pinkie fingers to explore the pattern. Once they reached a decision about the orientation of the pattern, participants responded by pressing one of the two foot pedals (one for each orientation) that were counterbalanced across participants. This method ensured that all participants started the haptic exploration in the same way and explored the pattern using the same fingers. Moreover, although a green light indicated when to place the hand over the pattern and start the exploration, the actual beginning of each trial (in terms of response time measurement and event markers for EEG acquisition) was determined by an automatic signal sent to the computer at the first contact of the participant's hand with the stimulus (cylinders were touch sensitive and sent the signal to the EEG computer immediately after the first contact with any cylinder). This allowed us to accurately control the extent of the haptic exploration and the response times for all participants, regardless of the delay between the onset of the led light and the first contact with the stimulus. Once the trial finished, the participants were instructed to rest the hand on the side of the presentation platform while the experimenter configured the next trial.

After a practice phase that ended only after participants perfectly understood the task and all the procedures, participants performed a total of 112 experimental trials divided into two blocks of 56 trials each with a 5-minute resting interval between blocks. Upon completion of the task, participants were debriefed.

2.4. EEG pre-processing and epoch rejection

A 34-channel elasticized Quick-cap with Ag/AgCl sintered electrodes (Neuroscan Medical supplies, Inc.) was used to record EEG data from scalp electrodes (FP1, FP2, F7, F3, FZ, F4, F8, FT9, FT7, FC3, FCZ, FC4, FT8, FT10, T3, C3, CZ, C4, T4, TP7, CP3, CPZ, CP4, TP8, T5, P3, PZ, P4, T6, P01, P02, O1, OZ, O2) positioned according to the extended international 10-20 system (American EEG society, 1991). To control the influence of ocular artifacts, vertical (VEOG) and horizontal (HEOG) electro-oculograms were recorded in two bipolar channels. Eye blinks and vertical eye movements were monitored via electrodes located below and on the supra-orbital ridge of the left eye. Horizontal artifacts were monitored via electrodes on the outer canthus of each eye. Linked mastoids (A1 A2) were used as reference and participants were grounded to the AFz electrode. All data were digitized using a NuAmps amplifier (Neuroscan Inc.) in continuous recording mode. Sampling rate was 250Hz and all channels were online band-pass filtered (0.1-70Hz) and notch filtered (50Hz) to eliminate power line artifacts. The overall impedance was maintained below $5k\Omega$. Prior to the task, participants were shown their ongoing EEG on the computer screen to teach them how to avoid eye blinking, jaw clenching and body movement artifacts.

Offline data preprocessing and analysis of the EEG recordings was performed using the EEGLAB toolbox (Delorme & Makeig, 2004) and ERPLAB plugin for EEGLAB (Lopez-Calderon & Luck, 2014), both running under MATLAB environment (The MathWorks, Inc.). Continuous data were filtered offline using a

digital FIR (finite impulse response) filter (1-30 Hz; 12 dB/oct. roll-off). Combination of low-high cutoffs and filter order (12 dB/oct. roll-off) were selected to increase statistical power by removing the maximum amount of noise while causing minimal distortion of the data (using the lowest order that eliminates low and high frequency artifacts without resulting in excessive attenuation of target frequencies). After filtering, data were separated into baseline corrected and nonoverlapping epochs time-locked to the haptic exploration onset, ranging from 1000 ms before to 3000 ms after the first contact of the participant's hand with the tactile pattern, with the pre-stimulus interval (1000 ms) as baseline period. Epoch rejection was performed in a semi-automated way. First, we visually inspected the epoched data to eliminate epochs containing high amplitude/frequency and other irregular artifacts but retaining stereotypic artifacts in the data. We then conducted infomax extended ICA decomposition (see Section 3.2 for details) using the runica algorithm implemented in EEGLAB (Lee, Girolami, & Sejnowski, 1999). The activities and scalp maps of the resulting independent components (ICs) were then plotted and visually inspected to identify artifactual components. Low frequency and high amplitude components with scalp topographies centered over the VEOG and HEOG sites were noted and rejected as blink and eye-movement related artifacts respectively. Components with focal topographies and increased activity in the range of 20-30 Hz were noted and rejected as muscle activity (EMG) artifacts (Mognon, Jovicich, Bruzzone, & Buiatti, 2011; Sebastián & Ballesteros, 2012). Then, we again visually inspected the pruned datasets and rejected any artifactual epochs remaining. Finally, a second ICA decomposition was performed on the artifact free epochs and the resulting weights were saved for averaging and posterior analyses. This resulted in an average of 96 ICA-pruned epochs per participant (min = 73, max = 104).

3. Data Analysis

3.1. Analysis of behavioral data

We used two dependent measures to evaluate behavioral performance: (1) The mean response times (RTs) corresponding to correct responses computed as the time between the first contact with the stimuli and the participant's response, and (2) accuracy of the orientation detection task.

Preliminary exploratory analysis of accuracy data showed deviations from a normal distribution in this dependent variable. Accuracy showed a pronounced positive skewness. We therefore transformed accuracy data (proportion of errors) by replacing proportions that were equal to 0 with 1/4n (where n is the number of observations on which the proportion is estimated for each group) and then applying an Arcsine (angular) transformation $\theta = sin^{-1}$ (\sqrt{p}), to fit normally distributed data on proportions and percentages that follow the binomial distribution (Anscombe, 1948).

Participants' RTs above and below 3 times the standard deviation were removed from the analysis. Overall, 2.25 trials (range 0 to 4) were removed from each participant (2.14% of the total of valid trials).

3.2. Independent component analysis (ICA) and component clustering

This study used EEGLAB to decompose the N channel EEG signal into N temporally independent components arising from distinct brain and non-brain sources (Bell & Sejnowski, 1995; Makeig, Bell, Jung, & Sejnowski, 1996). According to the authors, the use of ICA to decompose the signal is based on two

assumptions: (1) The EEG signal at a given electrode is a linear sum of temporally independent sources from spatially fixed locations; (2) volume conduction does not involve significant time delays in the spatial spread of the electric current (Jung et al., 2001). This linear combination can be reverted to find an unmixing matrix, **W**, in the equation **u** = **W**x, where **u** is the source matrix and **x** is the scalp EEG. We used the default extended-mode runica training parameters (Lee et al., 1999), an extension of the original algorithm of Bell and Sejnowski (Bell & Sejnowski, 1995) and stopping weight change set to 1e – 7. The extended mode makes it possible to separate a wider range of source signals (both super- and sub-Gaussian) maintaining simplicity, while the conservative stopping learning criterion lengthens ICA training, enabling cleaner and more reliable decompositions, particularly with more than 33 channels and a limited number of epochs. After submitting epochs to ICA decomposition, artefactual components were removed by inspection of their scalp topography and spectral power as detailed in Section 2.4.

Spatial localization of the remaining ICs was analyzed using the DIPFIT2 toolbox (Oostenveld & Oostendorp, 2002) (available from sccn.ucsd.edu/eeglab/dipfit.html). This tool attempts to spatially locate the cortical source of a given IC by hypothesizing a dipole source that could generate the scalp map potential distribution, compute a forward model that accounts for the maximum amount of variance in the scalp map, and represent it by three-dimensional coordinates (x, y, z). For each IC, a best-fitting single equivalent dipole was localized using a boundary element head model (BEM) where electrode coordinates where warped into. Next, to identify similar ICs in the orientation detection task across participants, the ICs of the 12 subjects were grouped into

clusters based on similar dipole locations, scalp topographies and event-related spectral perturbations (ERSPs) using the STUDY function of EEGLAB. In this study, the parameters of the clustering function were selected combining three different criteria: 1) The objectives and EEG measures selected; 2) the empirical evaluations of different parameter combinations along with recommendations from the EEGLAB developers and advanced users (which include using all types of information available, controlling the relative influence of each factor and keep the number of dimensions around 20); and 3) the clustering procedures employed in previous haptic studies using IC-clustering (Lin, Shaw, Young, Lin, & Jung, 2012). Prior to clustering, ICs outside the brain volume and those with residual variance above 30% were removed. For the remaining clusters, the clustering procedure was performed using the following steps: 1) To construct a common measure to specify the 'distances' (in a N-dimensional space) between ICs for their use by the clustering algorithm, scalp topography and ERSP were computed along with dipole source location; 2) ERSP and scalp topography measures were compressed and combined into a 10-dimensional vector each, due to the limitations of the EEGLAB pre-clustering algorithms and the redundancy of the data (e.g. around 3000 time/frequency ERSP values) using principal component analysis (PCA), while dipole location was combined into a 3-dimensional vector (x, y, z), resulting in a combined position vector (that account for the 'distances' 23-dimensional between ICs); 3) these measures were normalized by dividing the measure data of all PCAs by the standard deviation of the first principal component of the specific measure. The dipole location measure was then weighted by a factor of 10, ERSP measure by a factor of 3 and scalp topography by a factor of 5. Independent components more than 3 standard deviations away from cluster centroid were

removed. Finally, the EEGLAB k-means algorithm was applied to the combined measure to obtain 23 maximally distinct clusters. As this study aimed to explore the brain processes implicated in haptic sensorimotor and perceptual processes, we identified and selected clusters located in left and right sensorimotor cortices that were characterized by the presence of μ rhythm (with spectral power peaks around 10 and 20 Hz), parietal located clusters characterized by α rhythm (8-14 Hz), as well as occipital α clusters (8-14 Hz), to examine the implication of motor, sensory, spatial and visual processes in haptic grouping. These clusters were selected according to their location (visual inspection of the equivalent dipoles and scalp maps, along with the Talairach coordinates of the cluster centroid) and the ERSP activity found during the task.

3.3. Time frequency analysis and event-related spectral perturbations

To test the dynamics of the IC-clusters power spectra, epochs in each experimental condition were subjected to a time-frequency analysis in order to compute the event-related changes in power spectrum (ERSP) for each IC cluster over time (Makeig, 1993). All time-frequency analyses were performed on EEGLAB together with custom MATLAB scripts. Time windows were referenced to time 0, which denoted the first contact of the participant's hand with the haptic stimulus. The time window started at -1000 ms and ended at 2996 ms. Baseline spectral power was computed in the [-1000 -300] window. We removed the [-300 0] data interval to avoid including the perceptual effect derived by the onset of the green led that signals the start of the trial. After defining the window of interest, we computed the spectral power for each frequency, obtained the average across trials and plotted the results as relative changes in spectral log amplitudes from

the baseline (Sebastián, Reales, & Ballesteros, 2011). The ERSP was computed over 70 log-spaced frequencies (padding 8) from 8 Hz to 25 Hz and 200 time points. We used the complex Morlet wavelet approach (Tallon-Baudry & Bertrand, 1999), a method that provides a time-varying estimate of signal magnitude in each frequency band, offering a good compromise between time and frequency resolution, improving frequency resolution at higher frequencies compared to standard wavelet convolution (Delorme & Makeig, 2004). The wavelet family used in this study consisted of 8 cycles at the lowest frequency (8 Hz) with an expansion factor of 0.5, progressively increasing the number of cycles to 12.5 cycles at the highest frequency (25 Hz). Finally, we used single-trial baseline correction to compute mean ERSP for each individual trial (Gardony, Eddy, Brunyé, & Taylor, 2017). This method calculates for every trial and frequency, 200 complex vectors evenly spaced in time. The raw spectral power is calculated by squaring the length of this vectors. Then each power value is divided by the average power across trials in the baseline to obtain 200 power ratios. This power ratios are averaged to yield the mean proportional changes in spectral power relative to baseline. This proportion is finally log-transformed to obtain a measure of event related spectral changes in Decibels (dB) (Grandchamp & Delorme, 2011).

3.4. Statistical analysis

Behavioral data were analyzed using repeated measures *t*-test to explore statistical differences between proximity and similarity grouping conditions in both RTs and error rates (error rates were arcsine transformed prior to the analyses to meet parametric test assumptions as detailed in Section 3.1).

To deal with the multidimensionality of EEG data and the multiple comparison problem (familywise error rate), statistical analyses on the ERSP of the selected ICclusters were run using the Fieldtrip plug-in for MATLAB (Oostenveld, Fries, Maris, & Schoffelen, 2011), with non-parametric cluster-based permutation/Monte Carlo statistics, to determine the significant differences between grouping conditions. Time/frequency characteristics of all component epochs were first split into 2 samples (A and B) corresponding to the two experimental conditions; then the difference in means between these two samples was calculated (the observed value T). Next, A and B particular values were divided into two groups of size n_A and n_B in every possible way (every permutation of the two groups) and difference in sample means was calculated for each permutation to obtain the distribution of possible differences under the null hypothesis that the group label does not matter. Finally, *p*-values were calculated as the proportion of sampled permutations where the difference in means was greater than or equal to T. Finally, given that the present study focused on the differences between grouping conditions within predefined cluster locations (and not on the relative importance of these clusters for haptic grouping), all the statistical analyses were performed between grouping conditions within each cluster. Therefore, statistical tests between clusters were not conducted.

4. Results

4.1. Behavioral results

4.1.1. Response time (RT)

A paired-samples t-test was conducted on RTs for correct responses. The t-test revealed statistically significant differences between proximity and similarity grouping conditions [t (1, 14) = -3.78; p = .002; $\eta 2p$ = .506]. Participants detected the orientation of patterns faster when they were grouped by proximity (M = 1378 ms, SD = 222) than when they were grouped by texture similarity (M = 1920 ms, SD = 534) (see Fig 2a).

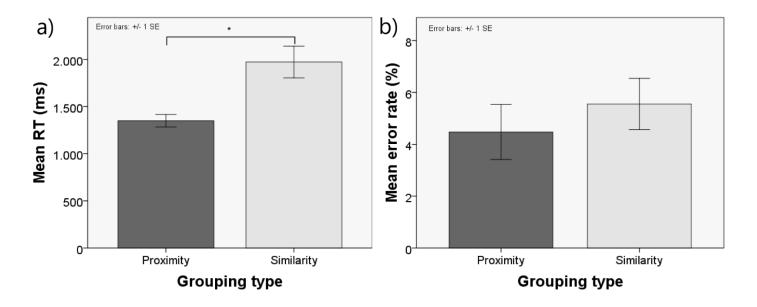


Figure 2. Behavioral results of the orientation detection task.

Mean response times (A) and percentage of errors (B) in the orientation detection task as a function of grouping type. Error bars represent the standard error of the mean (SE) over participants

4.1.2. Accuracy

A paired-samples t-test was also performed on the arcsine-transformed proportion of errors. No significant differences were found between proximity (M = 0.044, SD = 0.342) and similarity (M = 0.059, SD = 0.395) grouping conditions in error rate (see Fig 2b).

4.2. EEG dynamics

Three participants were eliminated from the EEG analyses due to the large number of artifacts, so all the EEG analyses were performed on the remaining 12

participants. We first removed bad channels and artefactual characteristics of the data, decomposed the remaining epoched EEG into spatially fixed and temporally independent components, eliminated artifactual ICs (eye and muscular artifacts) and fitted dipole models to the scalp topography of those components. The remaining ICs from the 12 participants (306 out of 432) were grouped into 23 clusters according to their dipole locations, scalp topographies and ERSP characteristics. This study aimed to explore the brain correlates of perceptual grouping in active touch, so in the following paragraphs, we will focus on and further analyze 5 component clusters located in or near left sensorimotor, right sensorimotor, left parietal, right parietal and occipital areas that showed relevant event-related spectral modulations during the task period. Fig 3 shows the scalp maps, dipole locations and power spectra of the selected components.

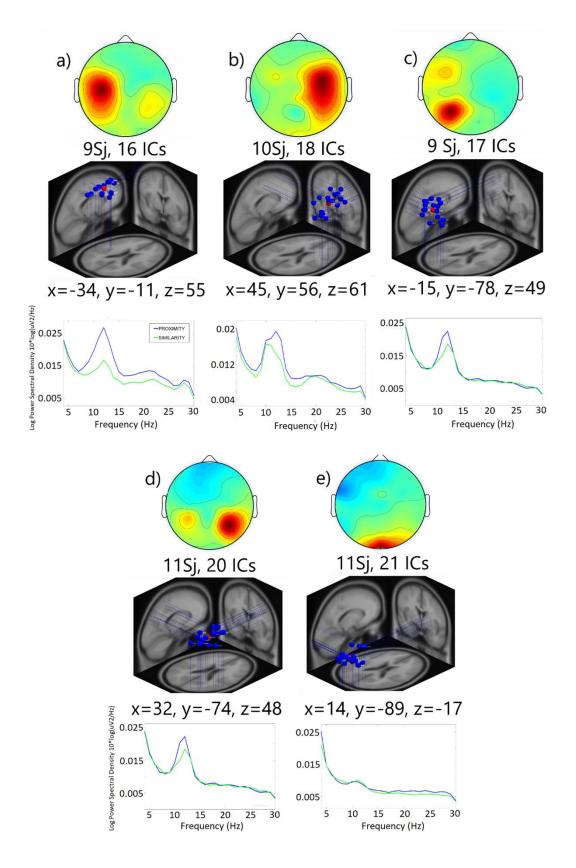


Figure 3. Characteristics of the 5 IC-clusters of interest.

Scalp maps, number of participants and constituent ICs, dipole locations, cluster centroid coordinates (Talairach & Tournoux, 1988), and power spectra for the 5 IC clusters of interest. From top-left to bottom right: a) left sensoriomotor, b) right sensoriomotor, c) left parietal, d) right parietal, e) occipital

4.2.1. IC-cluster Event-Related Spectral Perturbation (ERSP) and power spectra

To quantitatively analyze differences in oscillatory activity between proximity and similarity grouping epochs, ERSPs were plotted under both experimental conditions (see 3.3 Section) along with statistical differences between them. Four (left sensorimotor, right sensorimotor, left parietal and right parietal) out of five IC-clusters analyzed showed statistically significant differences between the two grouping conditions in ERSP during the time epoch analyzed. The occipital IC-cluster did not show significant differences between conditions in ERSP. See Fig 4.

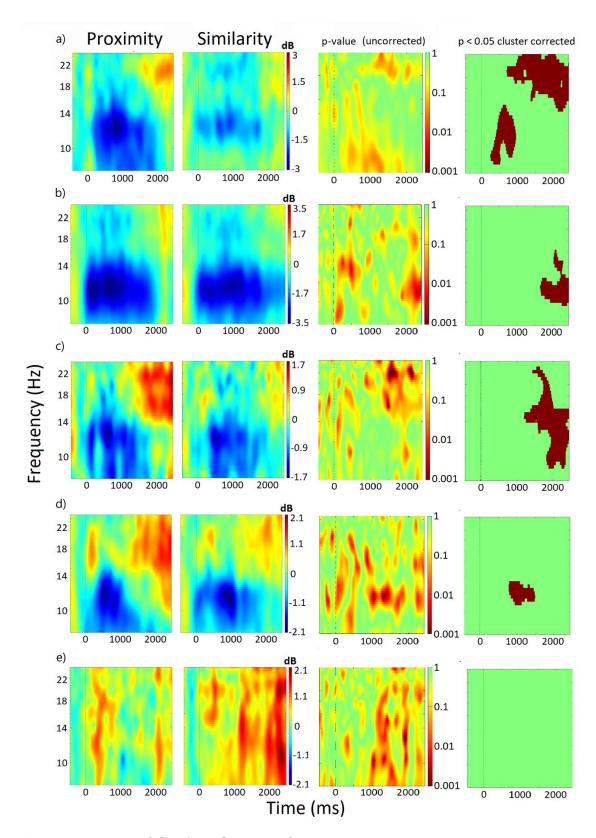


Figure 4. ERSPs of the 5 IC-clusters of interest.

Mean log-ERSPs (8-25 Hz) relative to stimulus onset (0) of the IC-clusters of interest for proximity (first column) and similarity (second column) conditions in the orientation detection task, along with uncorrected (third column) and cluster corrected (fourth column) p values. From top to bottom: a) left sensorimotor, b) right sensorimotor, c) left parietal, d) right parietal, e) occipital.

Fig 4a shows the ERSPs of a cluster of 16 ICs located in or near left sensorimotor scalp sites. Mean ERSP activity of the left sensorimotor IC-cluster for epochs in both proximity and similarity conditions shows an alpha band event-related desynchronization (ERD) time-locked to the beginning of the haptic exploration that was significantly more pronounced in the proximity condition within the 500-1000 ms time window. ERSP activity for this cluster also reveals an ongoing ERD in the beta band peaking around 20-22 Hz that was significantly more pronounced under the similarity condition. Last, proximity condition showed a greater event related synchronization (ERS) relative to similarity condition that starts approximately after the response execution (1500 ms).

Fig 4b shows the mean scalp map, ERSP and power spectra of a cluster of 18 ICs, located over the right sensorimotor cortex. Visual inspection of ERSP activity revealed an ERD in alpha and beta bands in both proximity and similarity conditions time-locked to the onset of the exploration. In addition, the statistical analysis showed that the alpha band ERD lasted significantly longer in the similarity than in the proximity condition.

Results from left parietal IC cluster (17 ICs) are displayed in Fig 4c. Both conditions exhibit an alpha band ERD that also extends to beta band. No differences in ERD between grouping conditions appeared, but the proximity condition showed an earlier and more pronounced resynchronization after ERD in both alpha and low beta bands.

ERSP from the IC cluster located over the right parietal cortex (20 ICs) indicate a greater alpha band ERD in the similarity condition around 1000 ms after the start of the haptic exploration (Fig 4d). Neither differences in ERS intensity nor timing in alpha and beta bands arise in this IC-cluster.

Finally, Fig 4e displays the scalp maps, ERSP and spectral power of an IC cluster located over the occipital cortex (21 ICs). Both conditions showed alpha and beta bands ERS during the task period in both frequency bands analyzed. No significant differences appeared between the experimental conditions.

5. Discussion

The present study was motivated by the lack of research considering both behavioral and electrophysiological data on the applicability of the perceptual grouping principles to active touch and their neural correlates. As far as we know, this is the first electrophysiological study to investigate the brain activity underlying perceptual grouping in the haptic modality using spatial proximity and texture similarity grouping principles. The study focused on event-related spectral perturbation, a measure that accounts for the time and frequency domains of the EEG signal (Lin et al., 2012; Martinovic, Lawson, & Craddock, 2012), and, specifically, in two frequency bands: alpha (8-14 Hz) and beta (15-25 Hz), which have been widely related to changes in brain activity in sensorimotor and parietal cortices (Gaetz & Cheyne, 2006; Melnik, Hairston, Ferris, & König, 2017; Pineda, 2005). To avoid confounds arising from the mixture of brain and non-brain activities obtained in scalp-recorded EEG signals, we used independent component analysis to decompose the EEG data into maximally independent components (Makeig et al., 1996), which were further analyzed via time-frequency analysis (Lin et al., 2012; Makeig, 1993). Overall, there were two main results: (1) Participants detected the orientation of stimuli grouped by proximity faster than those grouped by similarity, and (2) the IC-cluster ERSP analyses revealed a widespread bilateral activation of sensorimotor and parietal cortices, indicating: a) Selective alpha and beta band ERD over both ipsi- and contra-lateral sensorimotor and parietal areas, and a lack of involvement of the occipital cortex in haptic grouping during the orientation task; b) different timing of the alpha ERD/ERS pattern over those areas in the two different grouping conditions, mirroring the behavioral results; c) greater but shorter alpha and beta ERD over contra-lateral sensorimotor cortex in the proximity condition, possibly indicating the existence of different exploration demands centered in global (configurational) and local (individual) properties of proximity and similarity grouping respectively, and d) more pronounced alpha ERD over the right parietal cortex in the similarity condition, that could be related to the more demanding spatial integration processes in this condition. These results and their implications are discussed in detail below.

5.1. Faster responses to stimuli grouped by spatial proximity

As observed in previous visual studies (Han et al., 2001), participants responded faster to stimuli grouped by proximity than to those grouped by texture similarity. In the visual modality, this advantage has been linked to the dominance of holistic properties over component properties in the perceptual process (Kimchi, 1994; Kimchi & Bloch, 1998). According to this view, detecting the orientation of an array of elements (which in fact involves the detection of a global property) that are grouped by spatial proximity is faster because it could be considered as a holistic/configural property that relies on the relationship between individual components. On the other hand, texture could be considered a component property leading to higher RTs. The results of the present study suggest that comparable processes might occur in active touch. In particular, the spatial relation (the different distances) between the elements of the haptic pattern in the spatial proximity condition could also be considered as a holistic or

configural feature (Kimchi, 1994; Kimchi & Bloch, 1998; Pomerantz & Pristach, 1989). This feature describes a specific relation among the elements of the array rather than informing about the component itself; in other words, it gives information about the orientation of the pattern without the need to explore each element individually. On the other hand, a component feature like texture requires the identification of each element prior to the integration into a whole percept, thus leading to faster identification of patterns grouped by proximity than those grouped by similarity. While in visual modality the advantage of holistic/configural properties is thought to be related to spatial frequency analysis (Flevaris & Robertson, 2016), the differences found in the present study could be related to the different exploration demands in each grouping condition. When stimuli are grouped by proximity, participants can use the different spatial gaps in the global pattern to detect the orientation of the array without the need to identify and integrate the individual (local) characteristics of each element, thus leading to faster responses for stimuli grouped by proximity. By contrast, stimuli grouped by similarity would require the detection of the local component properties (texture) of each individual stimulus and integrate this information into a single object to come up with an answer. However, it is important to note that the proposed similarities between perceptual grouping in vision and haptics should be taken with caution. As we pointed out in the introduction, there are important differences in how the sensory information is acquired by each sensory modality (serial vs. parallel). Further investigation, including passive tactile tasks, would be necessary to draw solid conclusions about the commonalities between perceptual grouping in vision and touch.

5.2. Event-related spectral changes associated with different grouping conditions

The ERSP is thought to measure average dynamic changes in amplitude of the broadband frequency spectrum as a function of time relative to the onset of the task (Makeig, 1993). No statistical differences arose between epochs belonging to different conditions during the baseline, so we will only discuss ERSP and spectral power changes during the task period.

5.2.1. Left sensorimotor IC Cluster

The results of ERSP over the left motor cluster show an ERD in the alpha band that was more pronounced in the proximity condition between 500-1000 ms after the start of the task (see Fig 4a). This ERD was followed by an ERS that started approximately after the end of the task in each condition (1400 and 1800 ms respectively). Decreases in power/amplitude reflecting ERD in alpha band have been associated with high excitability states of the implicated areas (Klimesch, Sauseng, & Hanslmayr, 2007). In accordance with this view, the alpha ERD found over the left sensorimotor cluster is thought to be closely linked to active cognitive processing and may serve as an indirect measure of activity in those areas. The involvement of contralateral motor and sensory cortices in a haptic orientation task is not surprising given that these cortical areas, located at contralateral postcentral gyrus and pre-central gyrus, have been widely related to somatosensory perception, movement organization, voluntary hand movement, proprioception and contralateral finger and hand movements (Gazzaniga, Ivry, & Mangun, 2009). Thus, the greater (but shorter) alpha ERD in the proximity condition could reflect: (1) the distinct exploration demands required in the two different grouping conditions (see Section 5.1), and (2) the differential exploration and response times of proximity and similarity conditions that would be reflected here in the timing of the alpha ERD/ERS that mirrors the behavioral RTs.

A similar pattern of ERD/ERS emerged from beta band ERSP. While its functional role is not as well understood as other frequency bands, beta-band activity over sensorimotor areas has been related to motor control (Klostermann et al., 2007) and the maintenance of the current sensorimotor or cognitive state (Engel & Fries, 2010). Beta band is usually desynchronized with movement and recovers during immobility much faster than alpha rhythms, showing a stronger synchronization after the cessation of movements (Gert Pfurtscheller & Neuper, 1997). In accordance with this view, the differences between proximity and similarity conditions in beta-band activity over the left sensorimotor cortex seem to have a motor origin, possibly related to the shorter exploration times found in the proximity condition, with a transient ERD and a faster resynchronization in this grouping condition that seem to reflect the earlier cessation of the hand movements in this condition. These results are in line with previous findings that linked attenuated beta activity to voluntary movements across the motor-related brain regions, especially in the peri-rolandic region (Pfurtscheller & Neuper, 1997; Tzagarakis, Ince, Leuthold, & Pellizzer, 2010).

5.2.2. Right sensorimotor IC cluster

As seen in the left sensorimotor cluster, the right sensorimotor IC cluster exhibited alpha band ERD lasting significantly longer in the similarity condition, indicating the involvement of the ipsilateral sensorimotor cortex in the grouping task (Fig. 4b). ERSP activity within the beta band follows the same ERD/ERS

sequence as seen in alpha band, but no statistical differences appeared between conditions in this frequency band. Activity of ipsilateral motor and sensory areas usually accompanies the execution of unimanual tasks (Babiloni et al., 1999; Baraldi et al., 1999; Gross et al., 2005). However, the purpose of this involvement remains unclear (van Wijk, Beek, & Daffertshofer, 2012). It could be just a 'crosstalk' through projections between bilateral areas that facilitate the movement, or even the reflection of inhibitory processes that prevent involuntary movements (Gross et al., 2005; Sadato, Yonekura, Waki, Yamada, & Ishii, 1997; Stephan et al., 1999). Moreover, the strength of the involvement of ipsilateral sensorimotor areas correlates with task complexity (Hummel, Kirsammer, & Gerloff, 2003; Verstynen, 2004). Thus, the extended alpha ERD found in the similarity condition in this study could be an index of the greater difficulty/complexity of the similarity grouping condition that requires a more intense involvement of the ipsilateral cortex. However, it could also be that the differences arose from the longer exploration times in the similarity condition and the need to engage facilitatory and/or inhibitory processes for a longer period. Interestingly, the scalp topography shows a slightly more anterior location of the IC cluster, possibly involving the pre-motor cortex and supplementary motor area (SMA). Thus, the involvement of the ipsilateral cortex found in this cluster could be related to the online sensory control of the motor sequence and guidance of action. This would explain the ipsilateral beta-band desynchronization, as this activity is usually linked to motor functions (Engel & Fries, 2010), information transmission between the cortex and periphery (Davis, Tomlinson, & Morgan, 2012; Engel & Fries, 2010) and reciprocal connections between muscles and cortex (Baker, 2007). Overall, the results point to a motor origin of the ipsilateral sensorimotor cluster activity, related to the

online control of actions via sensory feedback (including inhibition of ipsilateral and facilitation of contralateral hand movements). This recruitment of ipsilateral motor areas was even greater (or at least longer lasting) in the similarity condition. A possible explanation is the greater requirements in terms of exploratory strategy and integration of individual elements in similarity condition. Alternatively, it is also possible that the greater alpha band ERD found in the similarity condition was a byproduct of the longer exploration times in this condition, an explanation that agrees with the slower RTs found in this condition.

5.2.3. Left parietal IC cluster

Modulations of the alpha band SMR during tactile tasks are usually widespread, showing a bilateral pattern that includes parietal regions (McFarland, Miner, Vaughan, & Wolpaw, 2000; Vukelić et al., 2014) that play an important role in the integration of somatosensory signals (Desmurget & Sirigu, 2009). Furthermore, the information flow from sensorimotor to parietal cortices within the alpha frequency range is thought to reflect the transmission of a copy of the efferent motor information essential to sensorimotor integration (Brovelli et al., 2004). The alpha band ERD found in the present study in contralateral parietal areas (Fig 4c) could reflect the cortical integration of the peripheral information acquired by the sensorimotor areas while performing the task. In the similarity grouping condition, with higher integration demands, participants need to explore each individual element, differentiate between two different textures (microspatial component) and integrate this information in order to detect the orientation of the patterns (macrospatial component), leading to greater ERD and later resynchronization (Zhang et al., 2005). In this line, Roland, O'Sullivan and Kawashima (1998) and

Kitada et al. (2005) using fMRI, found activation of the parietal cortex during roughness (microspatial) and shape/length (macrospatial) discrimination. In particular, Kitada et al. (2005) found increased activation of the parietal operculum and insula (including secondary somatosensory cortex) during a tactile roughness estimation task, two areas that have previously been linked to roughness discrimination (Greenspan & Winfield, 1992) and that have direct connections with the primary somatosensory cortex (Burton, Fabri, & Alloway, 1995). Finally, Karhu and Tesche (1999), providing electrical stimulation to the median nerve, discovered synchronized activity between neurons in primary and secondary contralateral somatosensory cortices (SI/SII). This finding suggests the involvement of SII and other cortices near the parietal operculum in the early processing of the somatosensory input. This finding is in line with the similar activation and timing found in the present study between somatosensory and parietal cortices. However, as we noted in the left and right sensorimotor clusters, we cannot discard the possibility that the increased activity found in the similarity condition was due to the longer exploration times in this condition. However, given that the differences between conditions seem to be due to the greater resynchronization in the proximity condition, an explanation based on the greater integration demands seems more plausible, as smaller resynchronization usually follows greater and more intense cortical activation (Klimesch et al., 2007).

5.2.4. Right parietal IC cluster

ERSP within the right parietal IC cluster followed an alpha ERD/ERS pattern similar to the one found in the right sensorimotor cortex. This result indicates the conjoint activation of ipsilateral right parietal and sensorimotor cortices as occurs

with the homotopic left areas. There has been converging evidence of right hemisphere dominance in spatial processing (D'Esposito et al., 1998). Particularly, right parietal activity has been linked to the integration of spatial information and coherent brain activity between parietal and motor cortices, and is thought to reflect the integration of sensorimotor behavior, especially when movements are guided by external haptic feedback (Blum, Lutz, & Jäncke, 2007). Thus, the increased activity in the right parietal IC cluster found in the present study might be related to the processing of the spatial characteristics of the task and the use of the resultant haptic feedback to guide the exploration movements (Serrien, Ivry, & Swinnen, 2006). The greater activation found in the similarity condition might be the result of the more demanding spatial integration processes required in this condition. The sensorimotor areas of the left hemisphere would use this information to modify the ongoing motor commands (Haaland, Elsinger, Mayer, Durgerian, & Rao, 2004). Another possible explanation is related to the role of the parietal cortex in tactile working memory. Li Hegner, Lutzenberger, Leiberg, and Braun (2007) found that ipsilateral temporoparietal activity, predominantly around SII areas, contributes to the maintenance of tactile pattern information in working memory. Given the previous findings of SII neurons involved in the perception of both roughness (Jiang, Tremblay, & Chapman, 1997) and orientation (Fitzgerald, Lane, Thakur, & Hsiao, 2006), it is plausible that the differences in alpha ERD in our study were associated with the greater sensorimotor demands of the similarity condition, as participants needed to process both micro-geometrical (integration of information about two different textures) and macro-geometrical (orientation) features (Bodegård, Geyer, Grefkes, Zilles, & Roland, 2001; Kaas, van Mier, Visser, & Goebel, 2013). In fact, right-hand discrimination of microgeometrical features specifically activates the right angular gyrus (Zhang et al., 2005), which is in line with the greater activation of the right parietal IC cluster in the similarity condition.

Finally, we cannot rule out the possibility of an attentional origin of at least part of the right parietal activity. The right temporoparietal junction (TPJ), as part of the ventral frontoparietal attention network, is actively involved in reorienting attention to salient stimuli (Corbetta & Shulman, 2002). Thus, it could be argued that patterns grouped by similarity entail a stronger attentional capture and/or focus, due to the presence of two different textures and the higher processing demands. However, while it is difficult to disentangle attention and working memory processes due to their functional overlapping (Awh, Vogel, & Oh, 2006), it is unlikely that the activity found in our study had an attentional capture origin, given that the alpha ERD in the similarity condition peaked around 900-1000 ms after the first contact with the tactile pattern, whereas activity derived from attentional capture would be confined to the first few hundred milliseconds after the onset of the task.

5.2.5. Occipital IC cluster

Analysis of the ERSP of the occipital IC cluster revealed not only the absence of alpha and beta band ERD but also the existence of ERS at occipital areas in both grouping conditions. This is consistent with a brain state of reduced information processing ('idling' state) and active inhibition that occurs within brain areas that are not relevant for the task (Pfurtscheller, 2001; Pfurtscheller & Klimesch, 1990). Given that our participants performed the haptic task with their eyes open, the significant synchronization over occipital areas may reflect inhibition of irrelevant

visual processing throughout the task. This appears to be inconsistent with studies that found activation of visual areas during haptic perception (James et al., 2002; Sathian, 2005). However, the implication of visual areas in haptic perception is related to macroscopic features such as object shape or 3D structure (James et al., 2002; Snow et al., 2014) as well as to object recognition (Amedi, Malach, Hendler, Peled, & Zohary, 2001). In the present study, the detection of orientation relied on micro-geometric features like texture discrimination and the spatial relation between scattered elements that did not conform to a familiar or a shape-defined object, a process that would not engage the visual cortex (Merabet et al., 2006).

Taken together, our results show the involvement of a bilateral network of sensorimotor and parietal areas in detecting the orientation of Gestalt grouped patterns in haptic modality. This is in accordance with previous haptic modality studies addressing orientation (Zangaladze, Epstein, Grafton, & Sathian, 1999; Zhang et al., 2005) and texture processing (Roland et al., 1998; Stilla & Sathian, 2008). These results are also in line with hemispheric specialization views that linked left hemisphere activity within sensorimotor and parietal areas (at least in right-handed participants) to movement organization and selection, and the integration of sensorimotor information; and right hemisphere activity to the use of sensory feedback to guide movements and to the process of the spatial components of sensorimotor processing, including those related to attentional orientation and working memory (for a review of hemispheric specialization and integration see Serrien et al., 2006). This view is in line with our electrophysiological results, linking the differences in alpha and beta band ERD/ERS in the left (contralateral) cortex to the control of voluntary movements and the integration of sensory information, and the differences in the right

(ipsilateral) cortex to the sensory-based guidance of the movement sequence and the spatial aspects of the task, including the integration of spatial information, maintenance of the information in working memory and orientation of attention.

5.3. Shortcomings, limitations and future directions

To the best of our knowledge, this is the first study to investigate the neurophysiological correlates of two key grouping principles in haptic perception. In this study, we used a more whole-hand exploration task instead of just a onefingertip exploration task. The haptic task was performed using a novel haptic device that resembles those used for visual perception. However, the study has some limitations that must be addressed in future research. First, the total number of trials was limited. This was due to the needed to manually configure the haptic pattern between trials by placing the cylinders one by one into the appropriate sockets before the beginning of each trial. Further improvements in the novel *MonHap* device would enable us to automate this process, allowing a considerable increase in the number of trials. This would yield reliable EEG recordings with more complex designs. Second, the serial nature of the haptic modality and the extent of the exploration times made it impossible to record evoked activity in addition to spectral ERSP activity, a limitation that is common in tactile experiments. Third, future studies should investigate the functional and causal connectivity between brain areas implicated in haptic perceptual grouping. We expect to observe an intense connectivity between active sensorimotor and parietal areas within and between hemispheres as shown in other haptic studies (Lin et al., 2012; Vukelić et al., 2014). Finally, our study did not address the question of how the grouping principles interact when two or more congruent or incongruent principles are present within the same stimulus. It would be interesting in future studies to include two or more grouping principles within the same trial. This would allow us to explore the pattern of facilitation and interference, as well as the dominance of one principle over another. This kind of interaction study, together with variations in the relative strength of each grouping principle, could provide a deeper understanding of the process of perceptual grouping in touch and the differences and commonalties with other sensory modalities.

6. Conclusions

To conclude, the present study replicates in the haptic modality behavioral findings in the visual modality, showing faster RTs for the stimuli grouped by proximity than for those grouped by similarity. Moreover, the analysis of ERSP activity shows the involvement of a bilateral network of parietal and sensorimotor areas in the processing of the grouped patterns, as indicated by the desynchronization of alpha and beta frequency bands during the task. From the analysis of the differences between epochs in which haptic patterns were grouped by proximity and by similarity, we can conclude that similarity grouping is related to more intense spatial integration processing due to the need to integrate microgeometrical properties (texture) of the stimulus in order to extract the macrogeometrical properties. This leads to greater processing requirements and more activity in areas implicated in the integration of sensorimotor information and spatial processing. Finally, the absence of reliable activation in occipital areas signals the lack of involvement of visual cortex in haptic perceptual grouping, at

least when the task involves only the processing of low level features such as roughness and orientation.

Haptic Perceptual Grouping: Behavioral and Neurophysiological Correlates

CHAPTER 7: INTFRACTIONS DYNAMICS BETWEEN GROUPING PRINCIPLES IN TOUCH: PHENOMENOLOGICAL AND PSYCHOPHYSICAL **EVIDENCE**

Haptic Perceptual Grouping: Behavioral and Neurophysiological Correlates

Interaction dynamics between grouping principles in touch: phenomenological and psychophysical evidence

Antonio Prieto, Julia Mayas and Soledad Ballesteros.

{antonioprieto@psi.uned.es, jmayas@psi.uned.es, mballesteros@psi.uned.es}

Departamento de Psicología Básica II, Studies on Aging and Neurodegenerative

Diseases Research Group

Prieto, A., Mayas, J. & Ballesteros, S. (2018). Interaction dynamics between grouping principles in touch: phenomenological and psychophysical evidence. Psychological Research. https://doi.org/10.1007/s00426-018-1029-0

Haptic Perceptual Grouping: Behavioral and Neurophysiological Correlates

Abstract

In two experiments, we investigated the interactions between the grouping

principles of spatial-proximity and texture-similarity in touch. For that purpose,

we adapted to touch two paradigms widely employed in vision. In Experiment 1,

we used an experimental phenomenological task consisting of rating the strength

of grouping in both acting-alone and conjoined cooperative and competitive

conditions. In Experiment 2, participants performed a psychophysical task in

which an objective (in)correct response was defined by selectively attending to

one grouping cue in different blocks of trials. The results showed that spatial

proximity dominated over texture similarity when the two principles were

conjoined in competition. In addition, the present results are compatible with an

additive model of grouping effects as indicated by the greater grouping effect in the

cooperative condition and the smaller grouping effect in the competitive condition

relative to acting-alone grouping principles. The similarities and differences

between vision and touch are discussed.

KEYWORDS: cooperation; competition; perceptual grouping; spatial proximity;

texture-similarity; touch, haptic

Agrupamiento Perceptivo Háptico: Correlatos conductuales y Neurofisiológicos

153

Haptic Perceptual Grouping: Behavioral and Neurophysiological Correlates

1. Introduction

Perceptual organization comprises a whole set of processes involved in how the human brain organizes the incoming stream of perceptual information to build coherent and relevant units that are the basis of integrated perception (Schmidt & Schmidt, 2013; Wagemans, Elder, et al., 2012). An important organizational phenomenon is perceptual grouping, which refers to the fact that observers perceive some elements of the scene as going together more strongly than others (Wagemans, Elder, et al., 2012). The study of perceptual grouping began with Wertheimer (1923) in the context of Gestalt psychology. In his seminal work, he described and developed the main factors involved in grouping the discrete elements of the perceptual scene.

During the second half of the 20th century, the topic of perceptual grouping was examined from the perspective of experimental psychology, leading to the description of a series of new grouping principles (Alais, Blake, & Lee, 1998; Palmer & Rock, 1994; Palmer, 1992; van den Berg, Kubovy, & Schirillo, 2011; Vickery, 2008), the quantitative measurement of grouping, and the establishment of laws and models that account for the grouping effects (Kubovy et al., 1998; Kubovy & Wagemans, 1995).

Even though the study of tactile perception has interested psychologists for a long time, and that important perceptual issues have been addressed within this modality from an experimental and neuroscientific approach (Ballesteros & Heller, 2008; Heller & Ballesteros, 2006), the studies involving perceptual grouping and its functioning mechanisms have focused almost exclusively on the visual and auditory modalities (see Wagemans, Elder, et al., 2012; Wagemans, Feldman, et al., 2012, for an extensive review). However, there has been recent renewed interest

in the study of perceptual grouping in the tactile modality (see Gallace & Spence, 2011, for a review of the history of perceptual grouping in tactile perception), challenging former claims about the lack of applicability of the grouping principles to touch (Révész, 1953), the difficulties related to its serial nature (Grunwald, 2008; Lederman & Klatzky, 2009), and drawing on the fact that some features such as surface texture and hardness are more salient for touch than for vision (Klatzky, Lederman, & Reed, 1987). Specifically, Chang, Nesbitt, and Wilkins (2007a, 2007b) found that participants grouped visual and tactile patterns in a similar way using different grouping principles. More recently, Overvliet, Krampe, and Wagemans (2012, 2013) found that proximity and similarity cues influenced contour detection and haptic search, respectively. Moreover, proximity grouping and certain configural cues speeded up the haptic search (Verlaers, Wagemans, & Overvliet, 2015; Overvliet & Plaisier, 2016). This body of work demonstrates that some grouping principles operate in the tactile modality and influence other cognitive processes, and that the laws that govern the processes of perceptual grouping in haptic and visual/auditory modalities could be comparable to some extent. This is consistent with previous research in touch, which found shared mechanisms between sensory modalities in a number of perceptual phenomena such as symmetry detection, perceptual illusions and repetition priming (Ballesteros & Reales, 2004; Ballesteros & Reales, 2005; Heller & Joyner, 1993).

The quantitative study of the interactions that occur when different grouping principles act conjointly have received considerable attention in vision. That is, when the combined principles act in *cooperation* (i.e., when the grouping principles are conjoined in such a way that they strengthen a certain stimulus configuration) or in *competition* (i.e., when the grouping principles operate against

each other, strengthening different stimulus configurations and producing ambiguous and unstable perceptual organizations) (Kubovy & van den Berg, 2008; Luna et al., 2016; Quinlan & Wilton, 1998; Schmidt & Schmidt, 2013).

This line of research has pursued two main objectives. The first was to find a model accounting for the observed separate and combined effects of the grouping principles. Specifically, Kubovy and van den Berg (2008) proposed an additive model of the grouping effects, which predictions can be tested under experimental conditions. According to their model, additive effects can be inferred if: (1) the grouping strength of the cooperation condition is greater than the grouping strength of either principle acting alone; and (2) the grouping strength when the two principles are combined in competition is weaker than either principle acting alone. The second objective was to identify the rules that determine which principles dominate the perceived organization when two grouping cues are combined (Han & Humphreys, 1999; Palmer & Beck, 2007; Schmidt & Schmidt, 2013). In this case, the classic rules of processing dominance are assumed (Navon, 1977, 1981; Pomerantz, 1983; Ward, 1983). Thus, a grouping cue will dominate the perceived organization if: 1) it produces faster and/or more accurate responses; 2) there is less interference from the competitive presence of the other cue; 3) it leads to greater improvement of the responses to the other cue when it is presented in cooperation; and/or 4) it is perceived under shorter exposure times.

Two main types of paradigm have been employed to achieve these goals. The first is the "experimental phenomenological method" (Kubovy & Gephstein, 2003) in which participants are asked to directly report spontaneous grouping without any specific instruction about what should be perceived. The second paradigm uses psychophysical tasks (Kubovy & Gepshtein, 2003; Palmer, 2003). This

requires the inclusion of an objective correct response by transforming the perceptual experience, either by forcing observers to judge certain aspects of the stimulus or by hindering their perception. In this case, perceivers engage mechanisms not involved in the natural perception of the scene. This method makes it possible to analyze performance in terms of accuracy and/or response times, at the cost of provide only indirect measures of grouping.

Given the lack of research addressing the laws that govern the interactions between the grouping principles in touch, the present study aimed to investigate quantitatively how different grouping cues interact during the process of perceptual organization to generate an organized tactile percept. The main objectives of the present study were: 1) to investigate the compatibility of the haptic data with an additive model of the effects of grouping principles; and 2) to examine the dominance dynamics of both single and conjoined grouping principles. This approach will allow us to test the facilitation effect of cooperative cues, the interference/inhibitory effects of competing cues, and whether performance in conjoined conditions could be predicted from performance in single condition.

To achieve these objectives, we conducted 2 experiments in which we confronted two well-known grouping principles: spatial proximity and texture similarity (Prieto, Mayas, & Ballesteros, 2014). In Experiment 1 we employed a phenomenological method consisting of a rating task to estimate the strength of grouping in single (acting alone) and conjoined (cooperative and competitive) conditions. The task was similar to one used previously in vision (Quinlan & Wilton, 1998). We expected that grouping would be strengthened when the two principles cooperate, leading to a more stable organization and higher ratings

relative to single grouping principles acting alone. By contrast, grouping would weaken when the two principles compete, resulting in an unstable percept. This would lead to lower scores on the rating scale. We also expected that the dominance of one grouping principle in the competition condition would be determined by the relative strength of the principles acting alone. If different relative strengths occurred, the strongest principle would win the competition. No dominance should be observed if the relative strengths were similar.

In Experiment 2, we employed a psychophysical method derived from one previously used in vision (Luna et al., 2016), in which a correct response was objectively defined. We hypothesized that if a grouping cue produces faster and more accurate responses, if there is less interference from a second competitive cue, or if it leads to greater facilitation when it is presented as a cooperative non-attended cue, it could be concluded that the grouping cue dominates the haptic perceptual grouping process. We also expected that the dominance dynamics would be congruent with the results of Experiment 1. If one grouping cue showed greater relative strength or dominated the ratings in the competitive condition in Experiment 1, then that grouping cue would dominate the grouping process in Experiment 2.

2. Experiment 1. Perceived phenomenological strength

In this experiment, we tested the phenomenological strength of perceptual organization when the grouping principles act alone or interact in a cooperative or competitive manner.

The experimental procedure consisted of a rating task in which participants were asked to rate the degree to which the central target grouped with either the

left or right cohort of flankers, using a 9-point scale. We followed the simple assumption that the participants' estimates of the strength of grouping reflect the interactions (cooperation and competition) between the grouping cues directly.

2.1. Method

2.1.1. Participants

Twenty students (3 males; age range: 19-48, mean age = 28.53, SD = 8.64) at the Universidad Nacional de Educación a Distancia (UNED) participated in Experiment 1 as part of a second-year course. Eighteen were right-handed and all had normal tactile perception and were naïve to the purpose of the experiment. Before the experiment started, participants completed a Spanish adaptation of the Edinburgh Handedness Inventory (Bryden, 1977; Oldfield, 1971) and signed an informed consent for participation in the study. The experimental protocol was approved by the Ethics Committee of the Universidad Nacional de Educación a Distancia and was in accordance with the ethical standards of the Declaration of Helsinki (Williams, 2008; WMA General Assembly, 1964).

2.1.2. Apparatus

We used a device specifically designed for haptic exploration (Haptic Monitor/MonHap) inspired by an apparatus used with monkeys (Fagot, Arnaud, Chlambretto, & Fayolle, 1992). It consisted of an opaque box with two platforms containing an array of 10 x 10 sockets in which the tactile stimuli can be plugged to create the desired configuration. It has two openings for the hands, allowing for single- and two-handed exploration of the tactile displays. The MonHap was interfaced with a computer to control for stimulus presentation, and to record the responses and exploration times (se Figure 1 left).

2.1.3. Stimuli

Each haptic display consisted of 6 touch-sensitive cylinders and 1 touch-sensitive cube that were specifically designed for the MonHap device (Figure 1 right shows the individual stimuli). The top of the cylinders was circular (13mm in height x 15mm in diameter), while the top of the cube was square (13mm in height x 15mm in width). As the participants only explored the top surface of the cylinders/cube, from now on we will refer to them as circles/squares. Some individual stimuli were covered with sandpaper to create a rough texture, while others retained their original smooth metallic texture. In each trial, the circles/squares were arranged in a single row of seven elements. The central stimulus (the target) was always a square. The other six elements were circular and were organized in two cohorts (right and left, made up of three elements each) that flanked the target.

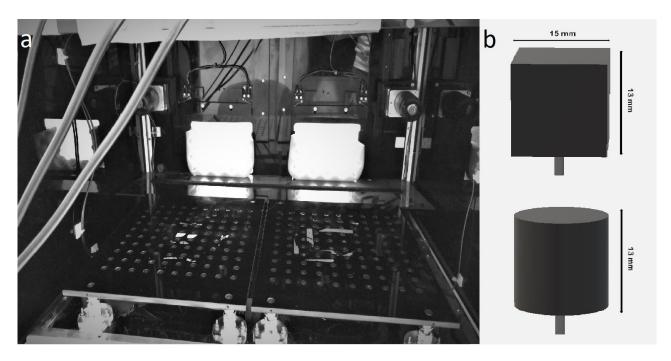


Figure 1. a) A view of the Haptic monitor; b) schematic representation of the touch-sensitive individual elements used in the haptic displays

A total of 18 different haptic displays were designed for the five different conditions shown in Figure 2. In the no-grouping displays (baseline), it was not possible to group the central target with the elements of the right or left cohort by means of any grouping principle. In the displays for grouping principles acting alone, the target could be grouped with the elements of the right (rightward display) or left (leftward display) cohort, by means of only one of the two grouping principles (proximity or texture similarity). In the two remaining conjoined conditions, the two principles were combined. In the conjoined cooperative displays, the two principles acted together so that the target could be grouped with the elements of either the right or the left cohort. In the conjoined competing displays, each principle competed to group the target with the elements of the right and left cohort, respectively. In the displays containing different proximity conditions, the distance between spatially close elements was 6 mm, while the distance between the spatially distant elements was 24 mm. In the displays containing only different texture similarity conditions, the distance between the elements was set at 6 mm.

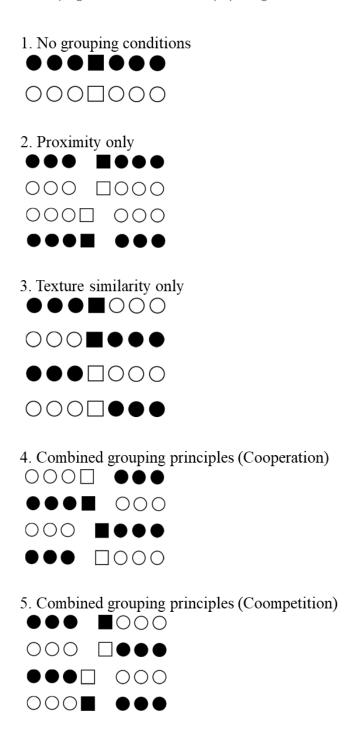


Figure 2. Representation of displays for all the conditions in Experiment 1: (1) no grouping; (2) proximity only; (3) texture similarity only; (4) cooperation between grouping principles, and (5) competition between grouping principles

2.1.4. Design and procedure

A single-factor repeated measures design was used, including the withinsubjects factor *grouping condition* with four different conditions: proximity and similarity acting alone, and combinations of these two grouping principles, either in cooperation or in competition.

At the beginning of the experimental session participants received verbal instructions. They also received comprehensive written instructions on the computer screen before the experiment started.

Participants were tested individually in a quiet and dimly lit room of our laboratory. The task consisted of rating the degree to which the target (the central square element) could be grouped with either the left or the right cohort of elements using a 9-point scale. Participants indicated verbally a number between 1 and 9. They were informed that a value of 5 represented the feeling that the target did not group with either the left or the right cohort. Ratings below 5 indicated that the target tended to group with the right (counterbalance 1) or the left (counterbalance 2) cohort of elements. Ratings above 5 indicated that the target tended to group with the left (counterbalance 1) or the right (counterbalance 2) cohort of elements. Participants were asked to consider the numerical distance from the central point of the scale as being directly proportional to the perceived grouping strength.

During the experimental session, participants were comfortably seated in front of the haptic device with their dominant hand introduced through one of the two apertures of the apparatus to explore the haptic stimuli. As participants could not see inside the device, the experimenter guided their hands to the start position before the beginning of each trial (the edge of the right hand placed near the stimulus without touching it). A green led light placed in front of the participant's eyes signaled the start of the trial. Participants were instructed to place their index and middle fingers at the beginning of the row, exploring the pattern sequentially

without stopping or going back, and give a verbal rating. The beginning of the trial was determined automatically by the first contact of the participant's hand with the stimulus. The cylinders were touch sensitive and sent a signal to the computer immediately after the first contact with the stimulus. At the end of the trial, the next random-generated stimulus was displayed on the computer screen. The experimenter registered the participant's answer on the response sheet and configured the next haptic display by plugging the stimuli on the presentation platform. The participants then started the new trial. This procedure was repeated until the 90 experimental trials were completed (10 baseline trials plus 20 trials in each of the four grouping conditions). In addition to the counterbalanced rating scale, half of the participants in each counterbalanced group explored the haptic stimulus starting from the left side of the haptic display (left to right exploration), while the other half started the exploration from the right (right to left exploration). Participants completed 4 to 8 practice trials before the start of the experimental session until they understood the experimental procedure. The whole experimental session lasted about 45 minutes.

2.2. Results

The data from one participant was not entered into the data analysis due to lack of understanding of the instructions. Prior to the statistical analyses, the raw scores were transformed following the procedure described by Quinlan and Wilton (1998). We collapsed the data from rightward and leftward displays and from the different rating-scale counterbalances to compute a measure reflecting the perceived strength of grouping in the direction of the designated dominant cohort. For example, 4 and 6 indicate the same strength of grouping in the two cases, even though each response reflects grouping in different absolute directions, depending

on the type of display (rightward or leftward) and the specific scale counterbalance (1-9; 9-1). Therefore, in the displays for grouping principle acting alone, the dominant cohort was defined by the grouping principle itself (same texture as the target in similarity displays and nearest to the target in proximity displays). In the conjoined cooperating displays, the dominant cohort was defined by the conjoined effect of the two principles. In the conjoined competing displays, the dominant cohort was established arbitrarily to the nearest cohort (proximity). Finally, in the no-grouping displays, the dominant cohort was established as the left cohort. Accordingly, individual rating scores were transformed to a scale ranging from -4 to +4, where the negative 4 reflects maximal grouping in the direction opposite to the dominant cohort, 0 reflects the absence of grouping in any direction and the positive 4 indicates maximal grouping in the dominant cohort.

2.2.1. Data for no-grouping condition (baseline)

First, we examined the data from the no-grouping condition to identify possible systematic response biases. Zero indicates absence of bias, whereas positive and negative scores indicate a bias toward the dominant and non-dominant cohort, respectively. Table 1 shows the transformed scores for each condition. The mean rating of the no-grouping condition was tested against a predicted value of 0 using one sample t-test. No systematic bias was found in the ratings [t_{18} = 1.80; p = .09; d = .41]. The inspection of the mean individual ratings showed that 16 out of 19 participants rated the no-grouping condition as 0, and the other 3 rated the no-grouping condition as 0.20, 0.30 and 0.20, respectively. These results suggest that there was no systematic bias. The data corresponding to the no-grouping displays were excluded from the remaining analyses.

Table 1. Summary of statistics for the different grouping conditions

Condition	Transformed mean rating	Standard deviation
No grouping (baseline)	.04	.10
Proximity	2.38	.80
Similarity	2.25	.80
Proximity O Similarity	3.40	.48
Proximity ÷ Similarity	.76	1.26

O, cooperation; ÷, competition

2.2.2. Data corresponding to the four grouping conditions

Figure 3 (left) represents the transformed ratings for the 4 remaining grouping conditions. We first tested the presence of any grouping effects by comparing the observed mean rating of each grouping condition with an expected value of 0 by using the one sample t-test. The effect of grouping was significant in all conditions: proximity only [$t_{18} = 12.98$; p < .001; d = 2.98], similarity only [$t_{18} = 12.24$; p < .001; d = 2.81], cooperation [$t_{18} = 30.97$; p < .001; d = 7.11] and competition [$t_{18} = 2.62$; p = .017; d = .60].

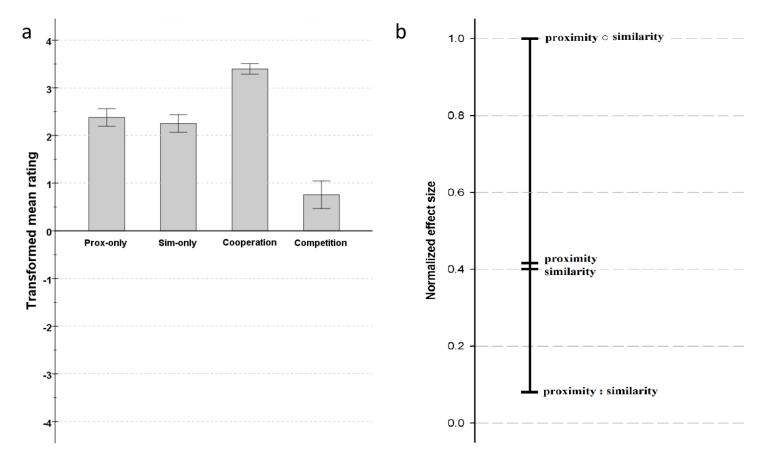


Figure 3. a): Transformed ratings for each grouping condition (the bars represent ±1 SE); b) normalized effect sizes used to examine the compatibility of the present data with additive effects of grouping principles (Kubovy & van den Berg, 2008). Cooperation between principles is identified by (o) and competition by (÷)

Next, to determine whether the grouping strength varied across the four conditions that showed significant grouping effects in the previous analysis, the transformed ratings were entered in a one-way repeated measure ANOVA with grouping condition as a fixed factor and participants as a random factor. The analysis showed a main effect of grouping condition [F₃, 16 = 29.76; p < .001; $\eta^2 p = .623$]. To compare the grouping effect size corresponding to the different conditions, the main effect was analyzed further using Bonferroni corrected post-hoc comparisons. These comparisons revealed that the two conditions with grouping principles acting alone produced similar grouping effects (p > .05). Conjoined cooperating principles produced greater grouping effects than actingalone conditions (all ps < .001) and conjoined competing principles (p < .001).

Finally, the competing principles condition had lower grouping effects than proximity (p < .001) and similarity (p = .016) acting alone and the conjoined cooperating principles condition (p < .001).

In sum, the data reveal that the greatest grouping effect occurred when the two grouping principles cooperated. When the two grouping principles acted alone, a significant and reliable grouping effect appeared, which was similar for the two grouping principles. Lastly, a small but significant grouping effect in the proximity direction was found when the two principles where pitted against each other. The general pattern of results obtained in touch indicates the existence of independent effects of grouping by proximity and grouping by similarity, as well as a combined effect of the conjoined principles that was slightly weaker than the sum of their separate effects and a little stronger than the difference between them.

Finally, an interesting finding was that the error bars in the competition conditions were larger than in the other conditions. A visual inspection of the individual ratings showed that while some participants tended to group by proximity (n = 14), others tended to group by similarity (n = 5). Thus, rather than cancelling each other out, the participants showed a preference for proximity or similarity grouping in their ratings, which is congruent with the greater variability seen in the competition condition.

2.2.3. Individual consistency

To further analyze the difference in score variability, we conducted an analysis of the participants' individual ratings, to provide additional information about the consistency of the scores in the different grouping conditions. To this end, we followed the strategy used in vision (Luna & Montoro, 2011). First, we conducted

homogeneity of variance tests (HOV) to compare the variances of scores in all conditions, using *t*-tests for the difference of variances in correlated samples (Zhang,1998).

$$t = \frac{S_1^2 - S_2^2}{\left[(1 - r^2) 4 S_1^2 S_2^2 / (n - 2) \right]^{0.5}}$$

Where S_1^2 = variance under one condition

 S_2^2 = variance under the other condition

r = correlation between conditions 1 and 2

n = sample size

The results showed that the variance in the competition condition was significantly higher than in the other grouping conditions (one-tailed t-tests, all ps < .05), while the variance in the cooperation condition was significantly lower than in all the other grouping conditions. Finally, no difference was observed in the variance in the acting-alone principle conditions (ps > .05). These results might reflect: 1) a lack of consistency in responses to the competitive displays, leading to inconsistent ratings not related to the individual strength of each grouping principle in the acting-alone conditions; or 2) greater inter-individual variability, resulting in some participants consistently grouping by proximity, and others consistently grouping by similarity.

We performed an additional analysis to test whether participants showed the same pattern of integration results for cooperation and competition conditions. Thus, we analyzed whether the participants who demonstrated a stronger proximity grouping effect in the acting-alone conditions also showed positive ratings in the competition condition, and whether the participants who demonstrated a greater grouping effect for the similarity grouping in the acting-alone conditions showed negative ratings in the competition condition. In the

cooperative displays, we tested whether the participants whose grouping scores were higher in the acting-alone conditions also had higher ratings in the cooperation condition. Next, we computed for all participants the bivariate correlation between the sum of scores in each acting-alone principle and the score in the cooperation condition; and the bivariate correlation between the difference in scores for each acting-alone principle and the score in the competition condition. A moderate significant correlation was found between the sum of the effects in acting-alone conditions and the grouping ratings in the cooperation condition (r = +.444, p = .03). Interestingly, a significant strong correlation was found between the difference in the acting-alone grouping effects and the competition condition (r = +.745, p < .001). These findings indicate that participants were generally consistent in their ratings, especially in the competition condition even though the score variability was higher. The participants who rated the grouping effects of proximity higher than similarity tended to have positive scores in the competition condition. On the other hand, participants who rated proximity lower than similarity tended to have negative scores in the competition condition. Thus, the increased variability in the competition condition does not seem to be attributable to the inconsistency of the competition condition ratings.

2.2.4. Compatibility with an additive model of grouping effects

To analyze the compatibility of the present data with the additivity of grouping effects, we followed the procedure used by Kubovy and van den Berg (2008) in their reinterpretation of the data from Quinlan and Wilton (1998). These authors pointed out that the key to infer the additivity of grouping principles in this kind of experiment relies on the effect found in the two conjoined conditions. First, to be

compatible with an additive model, the grouping effect of the two principles conjoined in cooperation must be greater than either of the two principles acting alone. Second, the grouping strength when the two principles are conjoined in competition should be smaller than the grouping effect of either grouping principle acting alone.

We normalized the data by using the effect size D instead of the mean transformed rating R (D = R/Standard error of R). Next, we adjusted the D values to fall between 0 and 1, by assuming the highest D value obtained as the 1 in the normalized scale and computing the rest of the normalized effect sizes as the ratio between the observed D value and the highest D value (D / highest D value observed) (Kubovy & van den Berg, 2008). The normalized results are shown in Figure 3-right and the inferences about additivity are listed in Table 2.

Table 2 Experiment 1. Inferences about the compatibility of the data with additivity of grouping

		Relation to additivity			
Data	Inference	Compatible	Not incompatible	Incompatible	
$D\left(p\mid 0\mid s\right) > D\left(p\right)$	The O combination of p and s is stronger than p	✓			
$D\left(p\mid 0\mid s\right)>D\left(s\right)$	The O combination of p and s is stronger than s	✓			
$D\left(p \div s\right) < D\left(p\right)$	The \div combination of p and s is not stronger than p	✓			
$D\left(p \div s\right) < D\left(s\right)$	The \div combination of p and s is not stronger than s	✓			
$D(p \circ s) > D(p \div s)$	The O combination of p and s is stronger than the \div combination of p and s	✓			
D (p O s) > D (p) > D (s) > $D (p \div s)$	The O combination of p and s is stronger than p , s and the \dot{z} combination of p and s	✓			

D represents the normalized measure of effect sizes; p, proximity; s, similarity; o, cooperation; \div , competition

The results show that the normalized effect sizes of each principle acting alone were very similar and fell between the two conjoined conditions. When proximity and similarity cooperated, the grouping effect was greater than that of each actingalone principle. On the other hand, when the two principles competed, the grouping effect was lower than either grouping principle acting alone.

3. Experiment 2

Experiment 1 showed that when the proximity and similarity grouping principles were conjoined in competition in a task in which participants were asked to directly report spontaneous grouping without specific instructions on what should be perceived, proximity dominated the resulting organization even when the two principles were equated in perceived grouping strength. Experiment

2 further explored which principle dominated the perceived organization when two grouping cues were conjoined in cooperation and competition. To this end, we examined the dominance dynamics of conjoined grouping cues, using a grouping paradigm in which participants had to discriminate the orientation (right or left) of groups based on two different cues presented in different blocks, similar to the one used in the visual modality (Luna et al., 2016). This paradigm introduces objectively correct responses by forcing the participants to perceive the grouped displays in a specific way (Han, 2004; Han, Ding, & Song, 2002; Palmer & Nelson, 2000).

We will focus on dependent measures of perceptual dominance used in previous visual studies (Navon, 1977, 1981; Pomerantz, 1983; Ward, 1983). Thus, a grouping cue will dominate processing if: 1) it leads to faster or more accurate responses; 2) there is less interference from the competitive presence of the other cue; and 3) it facilitates the response to the other cue when it is presented in cooperation with it.

3.1. Method

3.1.1. Participants

A new group of 20 students (5 males; age range: 20-45, mean age = 29.79, SD = 7.68) from the Universidad Nacional de Educación a Distancia (UNED) participated in this Experiment. The participants reported normal tactile perception and were naïve to the purpose of the experiment. As in Experiment 1, before the experiment started participants completed a Spanish adaptation of the Edinburgh Handedness Inventory (Bryden, 1977; Oldfield, 1971) and signed an informed consent form. The experimental protocol was approved by the local Ethics Committee and is in

accordance with the ethical standards of the Declaration of Helsinki (Williams, 2008; WMA General Assembly, 1964).

3.1.2. Apparatus and stimuli

The apparatus and stimuli were the same as those used in Experiment 1, except that the no-grouping condition was not included. Thus, a total of 16 stimuli were used in three experimental conditions: 1) acting-alone displays (single); 2) cooperative displays; and 3) competitive displays. Textures and distances between elements were the same as in Experiment 1 to ensure equivalent grouping strength of each cue.

3.1.3. Design and procedure

The 3 x 2 repeated measures design included two within-subject factors, grouping condition (single, cooperative, competitive) and directed attention (attention directed to groups based on proximity or texture similarity).

The experimental session lasted about 50 minutes, divided into two blocks of 20-25 minutes with a resting interval between them. The task consisted of discriminating the orientation (right or left) of groups based on different grouping cues (proximity and similarity) selectively attended to in different blocks of trials, while the other grouping cue was ignored. For example, in the proximity block, participants had to attend and respond only to the groups based on spatial proximity, while ignoring those based on texture similarity. By contrast, in the similarity block, participants attended and responded to groups based on texture similarity and ignored those based on spatial proximity.

The exploration instructions were the same as in Experiment 1, except that participants now used the index fingers of both hands to explore the stimuli. At the

beginning of each trial, participants placed their index fingers on either side of the tactile display in contact with the side of the cylinders without touching their surfaces. Next, they explored the surface of the patterns sequentially with both index fingers without stopping or going back, until the two index fingers touched, approximately in the center of the stimulus. Participants responded using the foot pedals located under their right (for right responses) and left (for left responses) feet. Participants were also asked to explore and respond as fast and accurately as possible, and to move their index fingers at the same time and the same speed.

RTs and accuracy were recorded as dependent variables. The number of experimental trials was 112, divided into two blocks of 56 trials with a rest interval between them. Participants completed 4 practice trials at the beginning of each block to ensure that they understood the experimental procedure. The order of the proximity and similarity blocks was counterbalanced across participants.

3.2. Results

3.2.1. Response time and error rates

The data from one participant were not included in the analysis because he reported a motor pathology that could interfere with speeded responses. Therefore, all the analyses were conducted on the remaining 19 subjects. Response times (RTs) to incorrect responses and those above or below 3 standard deviations from the mean were removed from the analysis. The remaining RTs and the error rates were analyzed in two separate repeated measures ANOVAs, with 2 x directed attention (proximity or texture similarity) and 3 x grouping condition (single, cooperative and competitive) within-subjects factors. The relevant data are summarized in Figure 4 and Table 3. All the analyses were Bonferroni corrected.

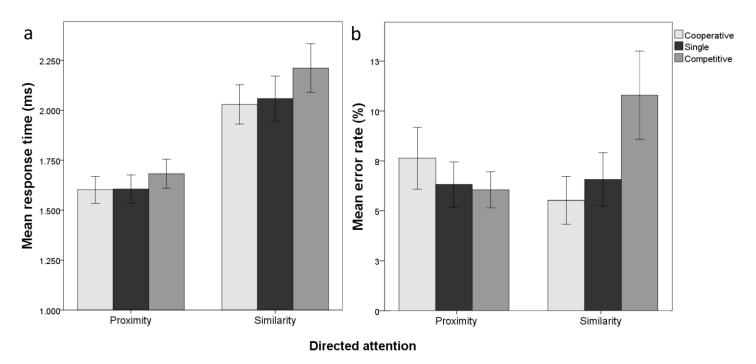


Figure 4. Mean response times in ms (a) and error rates in % (b) for directed attention and grouping conditions. The error bars represent ± 1 SE

Table 3. Mean response time (ms) and standard deviations (in brackets) for each condition in Experiment 2

Directed attention					
	Single	Coop.	Fac.	Comp.	Interf.
Proximity	1606 (307)	1602	-4 (103)	1683	77 (143)
		(293)		(318)	
Similarity	2059 (491)	2030	-29	2212	153 (147)
		(429)	(184)	(530)	
Advantage	453	428		529	

Fac.: cooperative RTs – single RTs; Interf.: competitive RTs – single RTs

The analysis of the RT data showed a main effect of *directed attention* [$F_{1, 18}$ = 36.15; p < .001; $\eta^2 p = .668$], indicating shorter RTs for proximity groupings (1630 ms) than for texture similarity groupings (2100 ms). The main effect of *grouping condition* also reached statistical significance [$F_{2, 17}$ = 36.15; p < .001; $\eta^2 p = .668$]. Pairwise comparisons indicated that responses in single and cooperative conditions were faster than responses in the competitive condition (p = .004 and p < .001 respectively). No other effects reached statistical significance.

The ANOVA conducted on error rates showed no significant main effects, but the interaction between *directed attention* and *grouping condition* was statistically significant [$F_{2, 17} = 4.49$; p = .018; $\eta^2 p = .199$]. Post-hoc comparisons revealed that participants committed more errors when the two principles competed in the similarity condition than when they competed in the proximity condition (p = .055). No other effects reached statistical significance.

3.2.2. Dominance dynamics and compatibility with additive effects

To further analyze the dominance dynamics obtained in this experiment and to compare the results with those of Experiment 1, we first transformed the raw RTs by computing a differential variable as follows: $I = conjoined \ condition$ (competitive or cooperative) – $single \ condition$. Positive scores indicate the magnitude of the interference (in ms) of the non-attended cue in the competitive condition, whereas negative scores indicate the magnitude of the facilitation effect when the two grouping cues act in cooperation. Table 3 summarizes the facilitation and interference scores. The facilitation/interference scores were then normalized using effect sizes $D \ (D = I/Standard \ error \ of \ I)$. The D values were adjusted to fall between -1 and +1, by taking the highest D value as 1 in the normalized scale and computing the rest of the normalized effect sizes as the ratio between the observed D value and the highest D value (D / highest D value observed). The 0 value in the scale represents the scores for the two single conditions. The normalized results are summarized in Fig. 5 and the inferences about additivity are listed in Table 4,

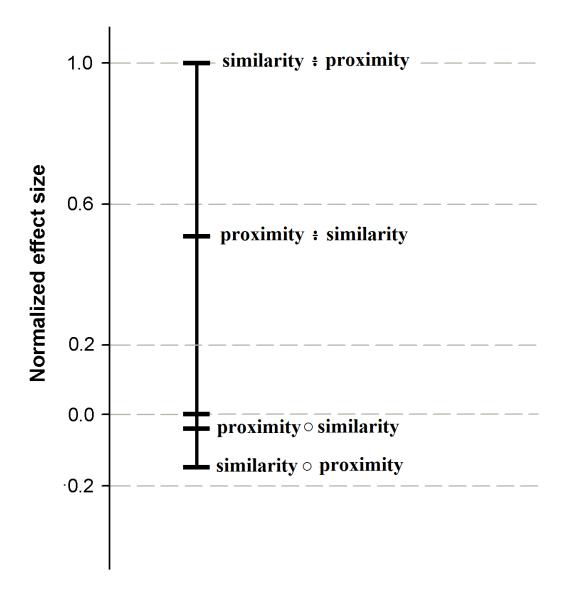


Figure 5. Normalized effect sizes used to examine the additivity of the data from Experiment 2. Cooperation between principles is identified by (o) and competition by (÷). The grouping cue on the left is the attended one, and the grouping cue on the right is the non-attended one. Positive scores indicate interference and negative scores facilitation.

Table 4. Inferences about the compatibility of the data from Experiment 2 with additivity effects of grouping.

		Relation to additivity		
Data	Inference	Compatible	Not incompatible	Incompatible
$D\left(s \circ p\right) > D\left(s\right)$	The O combination of s and p is stronger than s		✓	
$D(p \mid 0 \mid s) > D(p)$	The O combination of p and s is stronger than p		✓	
$D\left(s\div p\right) < D\left(s\right)$	The \div combination of p and s is not stronger than p	✓		
$D\left(p \div s\right) < D\left(p\right)$	The \div combination of p and s is not stronger than s	✓		
$D(p \circ s) > D(p \div s)$	The O combination of p and s is stronger than the \div combination of p and s	✓		
$D(s \cap p) > D(s \div p)$	The O combination of s and p is stronger than the \div combination of s and p	✓		
$D(p \circ s) > D(p) > D(p \div s)$	The O combination of p and s is stronger than p and the \div combination of p and s		✓	
$D(s \cap p) > D(s) > D(s \div p)$	The O combination of s and p is stronger than s and the \div combination of s and p		✓	

D represents the normalized measure of effect sizes; p, proximity; s, similarity; o, cooperation; \div , competition. The first grouping cue within parentheses is the attended cue, whereas the second is the non-attended (interfering/facilitating) cue.

The results of the normalized effect sizes show that when the two principles competed, the interference effect of the proximity cue over texture similarity (i.e., when proximity was the non-attended cue in the similarity block) was greater than the interference effect of the similarity cue over proximity (when similarity was the non-attended cue). The same pattern of results appeared in the cooperative condition. The facilitation effect obtained was greater when proximity was the ignored cue, although the effect sizes in this condition were considerably smaller.

In sum, the results of Experiment 2 were compatible with the additive model of grouping found in Experiment 1, and the tendency of proximity cues to dominate the organization of the haptic scene when the two grouping principles were in competition.

4. General discussion

The current study examined the interactive effects between two main grouping principles, spatial proximity and texture similarity in active touch. We investigated whether a grouping principle dominated the perceptual organization of the haptic scene. We also examined whether, as occurs in vision, the conjoined grouping effects in touch were compatible with an additive model.

Experiment 1showed grouping effects for both acting-alone grouping principles, which did not differ in strength. The grouping effect for the cooperative condition was stronger than the effect of each single principle alone. In addition, grouping effects occurred even when the grouping principles were conjoined in competition, although this effect was weaker than the effect of each principle alone. Interestingly, the positive scores indicate a faint dominance of proximity, even when the two principles were similar in perceived strength, as shown by the ratings in the acting-alone conditions (see Fig. 3-left). Following the criteria introduced by Kubovy and van den Berg (2008), our data are fully compatible with an additive model of grouping effects. Moreover, the consistency analyses showed strong correlations between the strength of the conjoined grouping conditions and the combination of single factor effects across participants. Based on these results, we can conclude that the greater variability found in the competitive condition was not a byproduct of the inconsistency of individual ratings, but the consequence of

the tendency of participants to group according to different grouping cues when the perceptual organization was vague and/or unclear. Supporting this conclusion, the analysis of the individual ratings in the competitive condition indicated that 14 participants grouped by proximity and 5 by similarity, which also explains the dominance of the proximity grouping when the two principles were confronted.

The results of Experiment 1 in active touch are in agreement with those obtained in vision by Quinlan & Wilton (1998) using a comparable task and similar grouping principles (spatial proximity and color/shape similarity). In touch as in vision, the perceived strength of grouping followed the same pattern, with the greatest grouping strength in the cooperative condition, followed by acting alone and competitive conditions. In addition, our results are compatible with an additive model of the grouping effects in touch according to the criteria introduced by Kubovy and van den Berg (2008). The main difference found in touch (Experiment 1) compared to findings in the visual modality was the dominance of the proximity grouping cue when both grouping principles compete. This result contrasts with the absence of dominance of proximity over similarity found by Quinlan and Wilton (1998) in their visual study. A possible explanation is that the single cues in their study were not matched in relative salience as they were in our study. Interestingly, Luna and Montoro (2011) conducted a visual experiment in which the relative salience of the grouping cues was previously equated. They compared several intrinsic cues with the extrinsic grouping principle of common region (Palmer, 1992). Their results showed that, when proximity and common region were pitted against each other, common region dominated the perceptual organization. This suggests that, although the laws that govern the interaction between these grouping principles in vision and touch share common ground, the

specific grouping principles that dominate the haptic and visual scene may differ, which is consistent with the fact that the most salient features in vision and touch differ (Klatzky et al., 1987).

Experiment 2 yielded similar conclusions. The dominance of grouping by proximity was explicit given 1) the significantly shorter RTs for groups formed by proximity, and 2) the higher error rate for groups formed by texture similarity in the competitive condition (proximity ignored), relative to groups formed by proximity (texture similarity ignored) in the same condition. Interestingly, single cues were responded to faster than competing cues, suggesting interference of the non-attended cue in both similarity and proximity blocks of trials. Thus, even when the instructions were to attend selectively to a specific grouping cue in each block and ignore the other, responses were slowed by the presence of a competing irrelevant cue in the haptic field, indicating that the non-attended cue was not completely inhibited and hindered motor responses (Luna et al., 2016). This interference effect disagrees with the dominance of proximity, given that it was bidirectional and symmetrical (same magnitude in both directions), as can be inferred from the absence of a significant interaction between the grouping condition and the attended cue. Despite this apparent contradiction, a further analysis of the normalized effect sizes showed that the effect size of the interference effect when proximity was the non-attended cue approximately doubled the effect size of the interference when texture similarity was the nonattended cue, a result that matches the difference between interferences scores. Thus, the normalization of the effect sizes reveals that the interference effect is better described as bidirectional but asymmetrical, fitting the previous evidence

concerning the dominance of spatial proximity in the perceptual organization of the haptic scene.

Experiment 2 also found a lack of facilitation effects of grouping principles acting cooperatively relative to grouping cues acting alone, which contrasts with the strong cooperative grouping effects found in the ratings of Experiment 1. These differences could be explained by the different nature of the grouping measures (direct vs indirect) and the different attentional demands of phenomenological and psychophysical tasks. In the phenomenological task used in Experiment 1, the participants were asked to rate the degree of grouping a central target with the elements on the right or left. No other instructions were provided, attention was deployed over the whole stimuli, and there was no time pressure. In the psychophysical task (Experiment 2), the participants had to explicitly attend to a specific grouping cue in each block of trials while performing the task as fast and accurately as possible. These differences in attentional requirements and time constraints could underlie the differences observed, reflecting different sensitivities in each task. In fact, this absence of facilitation in the cooperative condition has also been found in other tasks in which interference/facilitation effects are tested. Notably, MacLeod (1991) in his comprehensive review of the Stroop-like task literature (which shares the same characteristics as the psychophysical task employed in Experiment 2) said that even when facilitation exists, "this facilitation is much less than the corresponding interference in the incongruent condition" (MacLeod, 1991, p.174). The author argued that the most plausible reason for this result is the difficulty of speeding up a response that is already fast, which could account for the absence of reliable facilitation effects in our haptic study.

Finally, the normalization of the effect sizes (Experiment 2) allowed us to compare the compatibility of the data with an additive model of interactive grouping effects. As in Experiment 1, the results are compatible with an additive model based on the criteria mentioned above (Kubovy & van den Berg, 2008). Specifically, the acting-alone conditions fall between the two conjoined conditions. In addition, the order of the effect sizes was consistent with the postulated dominance of the proximity cue, with larger effect sizes in conjoined conditions when proximity is the non-attended irrelevant cue.

Taken together, several conclusions can be drawn from the results of the present study. First, the participants could spontaneously group the tactile patterns without any previous instructions in almost the same way as incidental/phenomenological grouping in the visual modality. This supports the idea that the internal perceptual grouping processes operate similarly in vision and touch. Second, the interaction pattern is fairly similar in the two modalities. This reinforces the conclusion that perceptual grouping follows the same rules in vision and touch. Third, spatial proximity seems to dominate the perceived organization of the haptic scene when grouping cues are confronted, even when the two principles have similar perceived strengths; making a clear difference with the results obtained in the visual modality (Luna & Montoro, 2011; Luna et al., 2016). Finally, the results support the compatibility of the interaction between proximity and similarity grouping principles in touch with an additive model.

5. Limitations and Future directions

The procedure presented here could be an important tool for the investigation of perceptual organization in touch. To the best of our knowledge, it is the first

attempt to adapt methods used widely in the visual modality, and to extend the systematic and quantitative study of the interactions between these two grouping principles to a previously neglected sensory modality. Future research should expand both implicit and explicit grouping cues under study and their combinations in order to obtain a representative amount of data. This will allow generalization of the present findings to draw a complete picture of the commonalities and differences between these two sensory modalities. Previous research in vision suggests that different grouping principles have different temporal courses and attentional demands (Ben-Av & Sagi, 1995; Ruth Kimchi & Razpurker-Apfeld, 2004). Thus, dissimilar patterns of interaction between different grouping principles in touch deserve further investigation. Future work should consider perceptual factors other than the classic grouping cues, such as perceptual completion (Nir & Ben Shahar, 2015), symmetry (Ballesteros, Millar, & Reales, 1998; Ballesteros & Reales, 2004), and statistical regularities (Dakin, 2015), in order to study the complex interactions between different factors involved in the organization of the haptic scene. Finally, a potential objective for future research is the development of new tasks to overcome the potential limitations of the paradigms used here. An interesting approach could be based on a combination of psychophysical tasks and indirect (or implicit) measures of grouping (Palmer & Beck, 2007). This kind of procedure combines the presence of an objective correct response with incidental grouping to avoid the use of alternative strategies, unrelated to perceptual grouping itself. In any case, beyond the (dis)advantages of each particular task, the use of a convergent approach based on multiple methods should be a fruitful strategy for the future study of perceptual grouping in touch.

6. Acknowledgments

The research reported in this article was supported by a Doctoral Fellowship from MECD granted to AP (FPU13/05914). It was also partially supported by grants from the Spanish Government (PSI2013-41409R) awarded to SB and from the Universidad Nacional de Educación a Distancia (2014-028-UNED-PROY) awarded to JM.

Haptic Perceptual Grouping: Behavioral and Neurophysiological Correlates

CHAPTER 8: BFHAVIORAL AND FI FCTROPHYSIOI OGIC AL CORRELATES OF INTERACTIONS BETWEEN GROUPING PRINCIPI FS IN TOUCH: **FVIDENCE FROM** PSYCHOPHYSICAL INDIRECT TASKS

Haptic Perceptual Grouping: Behavioral and Neurophysiological Correlates

Behavioral and electrophysiological correlates of interactions between grouping principles in touch: Evidence from psychophysical indirect tasks

Antonio Prieto, Julia Mayas and Soledad Ballesteros.

{antonioprieto@psi.uned.es, jmayas@psi.uned.es, mballesteros@psi.uned.es}

Departamento de Psicología Básica II, Studies on Aging and Neurodegenerative

Diseases Research Group

Prieto, A., Mayas, J. & Ballesteros, S. (2018). Behavioral and electrophysiological correlates of interactions between grouping principles in touch: Evidence from psychophysical indirect tasks. Neuropsychologia, (Under review).

Haptic Perceptual Grouping: Behavioral and Neurophysiological Correlates

Abstract

In two experiments we investigated the behavioral and brain correlates of the

interactions between spatial-proximity and texture-similarity grouping principles

in touch. We designed two adaptations of the repetition discrimination task (RDT)

previously used in vision. This task provides an indirect measure of grouping that

does not require explicit attention to the grouping process. In Experiment 1,

participants were presented with a row of elements alternating in texture except

for one pair in which the same texture was repeated. The participants had to

decide whether the repeated texture stimuli (similarity grouping) were smooth or

rough, while the spatial proximity between targets and distractors was varied

either to facilitate or hinder the response. In Experiment 2, participants indicated

which cohort (proximity grouping) contained more elements, while texture-

similarity within and between cohorts was modified. The results indicated additive

effects of grouping cues in which proximity dominated the perceptual grouping

process when the two principles acted together. In addition, the independent

component analysis (ICA) performed on electrophysiological data revealed the

implication of a widespread network of sensorimotor, prefrontal, parietal and

occipital brain areas in both experiments.

Keywords: Perceptual organization; proximity; similarity; grouping, touch

Agrupamiento Perceptivo Háptico: Correlatos conductuales y Neurofisiológicos

193

Haptic Perceptual Grouping: Behavioral and Neurophysiological Correlates

1. Introduction

Perceptual grouping plays a key role in the process of extracting information from the raw perceptual input, according to certain *cues* like shared features or spatial arrangement, and bound it together into an integrated percept (Schmidt & Schmidt, 2013). While the question was first discussed by Wertheimer (1923) in the context of Gestalt psychology (see Vezzani, Marino & Giora, 2012), it was not until the second half of the 20th century that it was addressed from the perspective of experimental psychology. The focus then was on the description of new grouping principles (e.g. Palmer, 1992), the quantitative measure of grouping, and the development of laws and models to account for grouping effects (Kubovy & van den Berg, 2008).

Most of the studies addressing the principles of perceptual grouping have been conducted on vision and audition (see Wagemans, Elder, et al., 2012; Wagemans, Feldman, et al., 2012 for extensive reviews). However, there has been increasing interest in the investigation and application of perceptual grouping to the haptic modality (see Gallace and Spence, 2011, for a review of the history of perceptual grouping in tactile perception). For example, Overvliet, Krampe, and Wagemans (2012, 2013) found that contour detection and haptic search are influenced by proximity and similarity grouping principles, respectively. More recently, Verlaers, Wagemans, and Overvliet (2015) and Overvliet and Plaisier (2016) reported that proximity grouping and configural cues speed up haptic enumeration. Thus, it seems that the tactile perceptual system organizes the information acquired by touch following laws and mechanisms similar to those used by other sensory modalities. In particular, Chang, Nesbitt, and Wilkins (2007a, 2007b) found that their participants grouped visual and tactile patterns in almost the same way. This

is in agreement with previous research in the haptic modality, which found similarities and shared mechanisms between vision and touch in a number of perceptual phenomena and cognitive processes, such as symmetry detection (Ballesteros & Reales, 2004), perceptual illusions (Ballesteros, Mayas, Reales, & Heller, 2012), haptic priming (Ballesteros & Reales, 2005).

In vision, considerable attention has focused on the interactions between different grouping principles when multiple cues act conjoined within the same stimulus; in other words, when the grouping principles act in cooperation (i.e., when conjoined grouping principles cooperate, strengthening certain stimulus configurations) and in competition (i.e., when conjoined principles compete against each other, strengthening different stimulus configurations) compared to when they act alone (Kubovy & van den Berg, 2008; Quinlan & Wilton, 1998). The results of these studies show that the grouping effects are stronger when the grouping principles cooperate. Moreover, when grouping principles compete, the grouping effect is weaker and unstable compared to their acting alone effect. Interestingly, Kubovy and van den Berg (2008) proposed an additive model of grouping effects that accounted for the results obtained in the visual modality. According to the authors, additive effects can be inferred when: (1) the grouping strength under cooperation conditions is greater than the grouping strength of each principle in isolation; and (2) the grouping strength under competition conditions is weaker than the grouping strength of each individual principle.

Other researchers have investigated the neural substrates of the interactions between the grouping principles in the visual modality. For example, Han (2004) recorded event-related potentials (ERPs) while observers performed an orientation identification task in which the grouping cues were congruent or

incongruent. Responses were faster to proximity-based orientation discrimination. In addition, responses were slowed by incongruent cues, and this effect was larger when the observers had to identify the orientation based on similarity cues while ignoring proximity. ERPs showed enhanced positivity over temporo-parietal areas in the 180-220 ms time window only under similarity conditions. These electrophysiological results provide evidence of the dominance of proximity over similarity grouping cues. However, the results should be taken with caution, as the relative strength of the grouping cues had not been equated. In a later work, Nikolaey, Gepshtein, Kubovy and Van Leeuwen (2008) varied the relative salience of the competing perceptual organizations using a phenomenological task,. Their results indicate that the ability to discriminate between competing organizations was correlated with the amplitude of C1 and P1 peaks. Unfortunately, there is no previous empirical evidence addressing the behavioral and neural correlates of the interaction between grouping principles in the tactile modality. To date, there have been only a few indirect approaches to the topic (e.g. Blankenburg, Ruff, Deichmann, Rees, & Driver, 2006).

Given the lack of studies addressing the interactions between different grouping principles in touch, the present study aimed to investigate the behavioral and brain (electroencephalographic, EEG) dynamics of the interactions when two grouping principles are conjoined either cooperatively or competitively. To achieve this objective, we conducted two experiments comparing two grouping principles, spatial proximity and texture similarity, in the haptic modality (Prieto, Mayas, & Ballesteros, 2014). The traditional paradigms used to measure the interaction between grouping principles usually involve tasks requiring either a phenomenological report of the strength of the grouping (Quinlan & Wilton, 1998)

or selectively attend to a grouping cue and perform speeded responses to indicate the perceived organization (Luna, Villalba-García, Montoro, & Hinojosa, 2016). The latter task introduces an objective, physically defined correct response, rather than a purely phenomenological one. This allows the assessment of performance (accuracy and response times) and of response bias against an objectively defined correct response, eliminating the possibility of spontaneous grouping without knowing what should be perceived. This could lead to the use of alternative strategies not related to grouping itself (Kubovy & Gepshtein, 2003). To avoid this problem, Palmer and Beck (2007) developed the repetition discrimination task (RDT), an indirect measure of grouping that does not require explicit attention to a grouping cue. The advantages of the RDT are: (1) that it provides a physically defined correct response, suitable to generate quantitative measures of grouping under speeded performance conditions; and (2) that it is apparently unrelated to grouping, preventing the strategic effects of directed attention tasks.

For the present study we designed two touch adaptations of the original RDT. These indirect haptic tasks require neither explicit attention to the grouping cues nor any knowledge about the purpose of the task. Importantly, the relative strengths of the grouping cues were equated by means of a phenomenological task in which participants rated the perceived strength of each grouping principle and their interactions (Prieto, Mayas, & Ballesteros, 2018). This ensured that any differences in the interaction pattern between the two grouping principles could not be attributable to the salience of a single cue.

In addition, to investigate the neural correlates (time/frequency oscillatory brain activity) of the interactions between grouping principles, we focused on alpha (8-14 Hz) and beta (15-25 Hz) band event-related spectral perturbations (ERSP)

within the sensorimotor cortex, which constitute the main components of the mu (μ) sensorimotor rhythm (SMR) (Vukelić et al., 2014). The enhancement and suppression of alpha-band power is considered an indicator of cortical inhibition/activation respectively, and is particularly useful to measure sensorimotor activity (Klimesch et al., 2007; Melnik et al., 2017). Beta band (ERSP), on the other hand, is associated with motor activity/performance and top-down sensory analysis (Boonstra, Daffertshofer, Breakspear, & Beek, 2007). Thus, the combination of μ -alpha and beta spectral changes could provide important information about haptic perceptual grouping. Additionally, we also focused on frontal and parietal ERSP as a marker of conflict resolution between competing cues (West, Jakubek, Wymbs, Perry, & Moore, 2005).

Based on previous findings obtained in vision and touch regarding the dominance of proximity (Han, 2004; Prieto et al., 2014), as well as in the similarities between these two modalities in perceptual grouping (Chang et al., 2007b, 2007a), we expected that proximity would dominate haptic grouping. Overall, we expected slower response times (RTs) and greater interference/facilitatory effects under competitive/cooperative conditions respectively when proximity was the interfering feature (Experiment 1, targets grouped by similarity). By contrast, we hypothesized slower RTs and less or no facilitation/interference at all when similarity was the interfering feature (Experiment 2, targets grouped by proximity). In addition, we hypothesized that the interactive effects of the grouping principles would be compatible with an additive model of grouping effects (Kubovy and van den Berg, 2008); in other words, (1) greater grouping strength under cooperative conditions compared to the strength of each principle

in isolation, and (2) weaker grouping strength under competition conditions compared to the strength of each principle alone.

Regarding the analysis of the ERSP, we expected the activation of a bilateral network of sensorimotor areas, that would be reflected in a power decrease (event-related desynchronization or ERD) of the alpha and beta bands over those regions during the task period (Melnik et al., 2017). We also hypothesized that conditions under which the two principles compete would lead to increased activity in frontal and parietal regions, traditionally associated with conflict processing and conflict resolution (Cohen & Ridderinkhof, 2013), especially when proximity was the interfering cue (Experiment 1), in accordance with the dominance of proximity expected in our behavioral hypotheses.

2. Experiment 1

Experiment 1 tested the influence of grouping by spatial proximity over the detection of targets based on texture similarity. Participants had to identify the repeated texture (target grouped by similarity) in a row of seven elements that alternated in texture. Proximity cues could either facilitate (cooperation condition) or hinder (competition condition) task performance.

2.1. Method

2.1.1. Participants

Twenty-one volunteer students (6 males; age range: 20-52, mean age = 34.60, SD = 9.24) from the Universidad Nacional de Educación a Distancia (UNED) participated in Experiment 1. All reported being right-handed, had normal tactile perception and were naïve to the purpose of the experiment. All the participants completed the Spanish adaptation of the Edinburgh Handedness Inventory (Oldfield, 1971)

and signed an informed consent form for participation in the study. The experimental protocol was approved by the Ethics Committee of the Universidad Nacional de Educación a Distancia and was in accordance with the ethical standards of the Declaration of Helsinki (Williams, 2008).

2.1.2. Apparatus and stimuli

We used a specially designed haptic device (Haptic Monitor, MonHap) for stimulus presentation and data acquisition (see Figure 1 left). The device consisted of an electromagnetically shielded (to avoid possible EEG artifacts) opaque box with two platforms containing an array of 10 x 10 sockets in which the tactile stimuli were plugged to create the desired configuration. The device had two apertures for the hands, enabling either single or bimanual exploration of the tactile patterns. The MonHap was interfaced with two different computers; one controlled the experimental sequence and stimulus presentation, and recorded responses and exploration times, and the other was used for the acquisition of EEG data.

The stimuli consisted of a series of touch-sensitive cylinders, each measuring 13 mm (height) x 15 mm (diameter), specifically designed for use in the MonHap device (Figure 1 right). The top surface of half of the cylinders was covered with sandpaper to create a rough texture. The other half had a smooth metallic texture. In each trial, the cylinders were arranged in a single row of seven elements to form 18 different stimuli configurations for three different conditions (see Figure 2). In cooperative trials, the targets were spatially close to each other (6 mm apart) and separated from the rest of the cylinders (24 mm), while in competitive trials, the targets were proximal to the distractors and non-proximal to each other. Finally, single (neutral) trials were those in which all the cylinders (targets and distractors) were equally spaced.

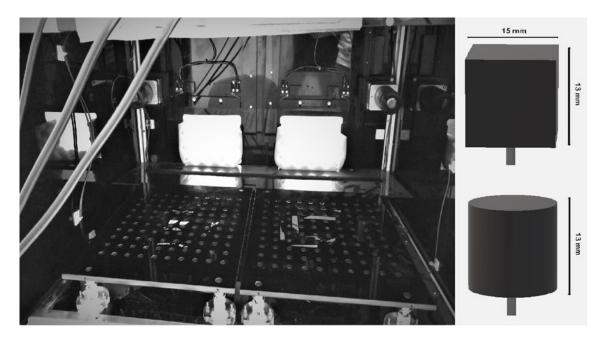


Figure 1. Left: An overall view of the Haptic monitor. Right: Schematic representation of the individual touch-sensitive elements that formed the haptic displays.

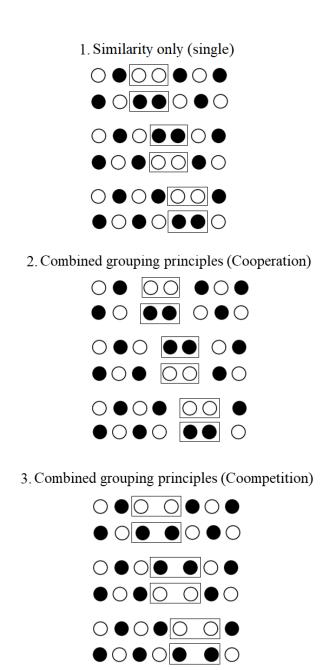


Figure 2. Representation of the three experimental conditions used in Experiment 1: (1) Similarity acting alone; (2) cooperation between grouping principles, and (3) competition between grouping principles. The circles inside the box are the target stimuli

2.1.3. Design and procedure

We used a 3 x 3 repeated measures design with two within-subject factors: 3 grouping conditions (cooperative, competitive, single) and 3 target positions (3/4,

4/5; 5/6). Response times from the first contact with the stimulus to the onset of the response and error rates were the dependent variables.

The experiment was conducted individually inside an electromagnetically shielded room of our laboratory. The participant received verbal instructions at the beginning of the experimental session. Once she/he was seated inside the experimental cabin, further instructions appeared on the computer screen. The task consisted of indicating as fast and accurately as possible if the repeated texture was rough or smooth. Participants explored the row of elements sequentially (from right to left) with their right hand and responded by pressing one of the two foot pedals (one for "smooth" and the other for "rough") that were counterbalanced across participants. The total number of trials was 108 (36 per condition), conducted in a single block that lasted approximately 40-50 minutes. Participants were seated in front of the haptic device with their right hand inside the right aperture of the apparatus. To minimize muscular artifacts produced by arm and body movements, they were instructed to put their forearms inside the device, and to rest comfortably on the back of the chair. The experimenter guided the hand of the participant to the start position at the beginning of each trial (the index and middle fingers of the right hand placed on the right side of the haptic display without touching it). Then, the experimenter signaled the start of the trial verbally. Participants were instructed to place their index and middle fingers on the surface of the first element of the row, to explore the pattern sequentially at a constant speed without going back and to respond as fast and accurately as possible using the foot pedals. In addition, the beginning of the trial (in terms of response time recording and EEG triggering) was initiated automatically by the first contact of the participant's hand with the stimulus, as all cylinders were touch

sensitive. At the end of the trial, the participant returned the hand to the start position and the computer automatically displayed the next randomly generated stimulus on the computer screen. The experimenter then configured the next trial by plugging the cylinders into the presentation platform. This procedure was repeated until the end of the experiment. Participants completed 10 practice trials before the start of the experimental session to ensure that they understood the experimental procedure.

2.1.4. EEG acquisition and pre-processing

We used a 34-channel elasticized cap with Ag/AgCl sintered electrodes (Neuroscan Medical supplies Inc.) to register EEG data from scalp electrodes (FP1, FP2, F7, F3, FZ, F4, F8, FT9, FT7, FC3, FCZ, FC4, FT8, FT10, T3, C3, CZ, C4, T4, TP7, CP3, CPZ, CP4, TP8, T5, P3, PZ, P4, T6, PO1, PO2, O1, OZ, O2) positioned according to the extended international 10-20 system. Vertical (VEOG) and horizontal (HEOG) were recorded in two bipolar channels to control for ocular artifacts. Blinks and vertical artifacts were monitored via electrodes below and above the orbital ridge of the left eye. Horizontal artifacts were monitored through electrodes located on the outer canthus of each eye. Participants were grounded to the AFz electrode, and linked mastoids (A1, A2) were used as the online reference. A NuAmps amplifier (Neuroscan Inc.) was used to digitize the data. Sampling rate was set at 250 Hz, overall impedance was maintained below $10k\Omega$ throughout the experimental procedure, and channels were online band-pass (0.1-70 Hz) and notch filtered (50 Hz) to eliminate power line and other artifacts. Prior to the start of the experiment, participants were shown their EEG on the screen and instructed how to avoid head and body movement artifacts.

Offline pre-processing of the EEG recordings was carried out under Matlab environment (The MathWorks, Inc), using the EEGLAB toolbox (Delorme & Makeig, 2004). Continuous raw data were filtered using a digital FIR (finite impulse response) filter (0.5-40 Hz; Order 32). We used the lowest order that eliminates low and high frequency artifacts while preserving target frequencies, in order to remove the maximum amount of noise while causing the minimum distortion of the data. After filtering, continuous EEG data were divided into baseline corrected and non-overlapped epochs ranging from 1000 ms before to 4000 ms after the start of exploration (the first contact of the fingers with the haptic display), with the pre-stimulus (-1000-0) interval as the baseline period. Epochs containing high amplitude/frequency and other irregular artifacts were removed by visual inspection. After that, artifact-free epochs were selected for averaging (Mean = 85 epochs per participant; Min/Max = 75-97). Importantly, the existence of ocular movements and/or muscular artifacts was not a criterion for epoch rejection. Instead, they were removed using Infomax Independent Component Analysis (ICA) decomposition (Bell & Sejnowski, 1995). The Details of the ICA analysis are described in section 2.2.2.

2.2. Data analysis

2.2.1. Behavioral data

Two dependent measures were used to evaluate behavioral performance: (1) mean response times (RTs) for correct responses, computed as the time between the first contact with the stimulus and the pressing of the foot pedal; and (2) accuracy of the task, computed as the proportion of errors in each condition. Two separate repeated measures ANOVAs with 3 *grouping conditions* (cooperative,

competitive, neutral) x 3 target positions (3/4, 4/5, 5/6) were conducted on RTs and accuracy, respectively. RT analysis was conducted only on correct responses within 3 standard deviations above and below the mean (7.62 % trials removed). All the statistical tests were Bonferroni corrected.

2.2.2. Independent component analysis (ICA) and component clustering To avoid the confound derived from the mixed EEG signals recorded from the scalp, we used EEGLAB to perform independent component analysis (ICA) (Bell & Sejnowski, 1995) on the EEG data. This enabled us to decompose the N-channel EEG signal into N temporally independent components (ICs) from different brain (and non-brain) sources (Makeig et al., 1996). This separation and identification of independent brain sources is essential to characterize the neuropsychological origins of the brain processes, and to relate a specific task with the activity and topography of those brain sources (Jung et al., 2001). We employed the runica extended mode training parameters (Lee et al., 1999), and a stopping weight change set to 1e - 7. The runica extension allows to separate out a wider range of source signals (super- and sub-Gaussian), while the selected stopping criterion lengthens ICA training. This makes it possible to obtain cleaner and reliable components, especially with the limited number of epochs in haptic studies. After completing ICA training and decomposition, non-brain and artifactual components were discarded by visual inspection of their scalp topography and power spectra (Makeig et al., 1997).

The topography of the remaining independent components (IC) was then analyzed using DIPFIT2, a plug-in for EEGLAB (Oostenveld & Oostendorp, 2002). This tool localizes equivalent dipole sources in a three-dimensional space (x, y, z), based on the location and activity of the scalp electrodes (we used a boundary element

model of the head). ICs were then clustered using the STUDY function of EEGLAB. First, we selected only ICs that contained less than 30% residual variance and were located inside the brain (139 clusters selected, approximately 8 clusters per participant). The clustering procedure was based on dipole location, scalp topography, spectral power and event-related spectral perturbation (ERSP), and was performed as follows: 1) scalp topography, spectral power and ERSP were pre-computed; 2) all the measures except dipole location were compressed into a 10-dimensional vector using principal component analysis (PCA); 3) dipole location was combined into a 3-dimensional vector (corresponding to the x, y and z coordinates), resulting in 33-dimensional combined measure space; 4) we normalized all the measures by dividing the measure data of all PCAs by the standard deviation of the first principal component in the specific measure. Before entering clustering, measures were weighted according to the desired magnitude of their individual contribution to the cluster process. Dipole locations were weighted by a factor of 10, ERSP and spectral power by a factor of 3, and scalp topography by a factor of 5. Finally, we applied the EEGLAB k-means algorithm to the combined measures to produce 8 maximally distinct clusters (independent components with locations more than 3 standard deviations away from the cluster centroid were removed from the resulting cluster). We analyzed only those component clusters located over sensorimotor, parietal and frontal regions that showed relevant ERSP modulations in alpha and beta bands during the task period. Therefore, the IC clusters obtained were selected to enter the posterior analyses according to the visual inspection of their topographies, the spectral activity, and the Talairach coordinates of the cluster centroid coordinates.

2.2.3. Time/frequency analysis of event-related spectral perturbations (ERSP) Event-related spectral changes in power spectrum (ERSP) for each IC cluster were computed over the entire epoch length in each experimental condition (Makeig, 1993). To avoid the inclusion of the brain activity arising from the verbal instruction that signaled the start of the trial, we employed the pre-stimulus interval -1000/ -300 ms as the baseline period. To estimate ERSP, we computed the power spectrum over a sliding latency window in each frequency band. Next, we calculated the average across trials and plotted the results as changes in spectral log amplitude relative to the baseline. Time-frequency analysis was performed using Fast Fourier Transform (FFT) with Hanning window tapering (Delorme & Makeig, 2004). This method provides time-varying estimates of the magnitude of the signal in each frequency band with a good balance between time and frequency resolution (Martinovic et al., 2012). All the time frequency analyses were carried out using EEGLAB functions along with custom scripts.

problem To deal with the multiple comparison arising from the multidimensionality and spatiotemporal structure of the electrophysiological data (Frehlich et al., 2016), we performed statistical analyses on the ERSP of the selected IC clusters using the Fieldtrip plug-in for MATLAB (Oostenveld et al., 2011) and the non-parametric cluster-based permutation/Monte Carlo statistics to determine the significant differences between experimental conditions. Time/frequency characteristics of all component epochs were first split into \mathbf{x} samples corresponding to the experimental conditions; the difference in means between these x samples was then calculated (the observed value T). Next, particular values were divided into groups of size n_x in every possible way (every permutation of the groups), and difference in sample means was calculated for each permutation to obtain the distribution of possible differences under the null hypothesis that the group label does not matter. Finally, *p*-values were calculated as the proportion of sampled permutations where the difference in means was greater than or equal to T. Post-hoc paired t-tests of related samples were performed where necessary.

2.3. Results

2.3.1. Behavioral results

Because of the randomized position of the target pairs, response times depended heavily on target position and scanning speed. To ensure that the scanning speed was the same across all conditions, we linearly regressed the data and fitted a regression line to compare the intercepts and slopes of each condition (Overvliet et al., 2012). A one-way repeated measures ANOVA showed no statistical differences between conditions in the intercepts or in the search slopes (all ps > .05), ensuring that any possible difference in response times were attributable to grouping manipulations and not to different scanning speeds or to different amounts of time to start moving the hand.

The 2-way repeated measures ANOVA conducted on the RTs yielded a main effect of target position [F (2, 19) = 122.19; p < .001; $\eta 2p$ = .859], indicating that RTs increased as a function of target position. Pairwise comparisons showed significant differences between all target positions (all ps < .001). The main effect of grouping condition was also significant [F (2, 19) = 20.459; p < .001; $\eta 2p$ = .506]. Pairwise comparisons showed that the mean RT for the single condition was faster than the other conditions. Also, the mean RT for the cooperative condition was faster than for the competitive condition. No other effects or interactions reached statistical

significance. The data from the raw RT analysis is plotted in Figure 3-left and Table 1 top row.

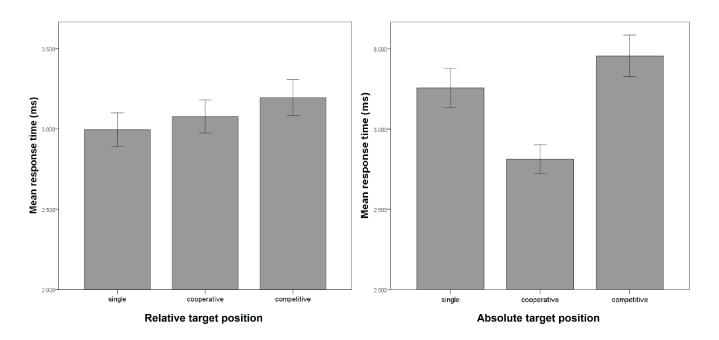


Figure 3. Left: Mean RTs (ms) for the three grouping conditions when the 3 relative target positions were collapsed. Right: Mean RT (ms) for the three grouping conditions corrected for the absolute target position (the bars represent ±1 SE).

Even though the relative position (in terms of number of elements) of the targets in the three conditions was the same (3/4, 4/5, 5/6; see Figure 2), the absolute position (in terms of distance from the beginning of the pattern) of a given target differed across the grouping conditions (e.g., if the target position was 3/4, the absolute distance from the stimulus start in the cooperative condition was greater than in the other two conditions due to the gap between the previous element and the target pair). To account for this difference in the target pairs across grouping conditions, we reduced the target positions to those that were comparable in terms of absolute distance, obtaining two absolute target positions (4/5, 5/6) corresponding to relative positions 3/4 and 4/5 in the cooperative condition, 4/5 and 5/6 in the neutral condition.

Next, we conducted a 2 absolute target position x 3 grouping condition repeated measures ANOVA on the RTs. As could be expected, the results showed a main effect of absolute target position $[F(1, 11) = -4.27; p = .001; \eta 2p = .624]$, indicating an increase in RT as a function of the distance between the target and the beginning of the haptic pattern. More interesting, the main effect of grouping condition also reached statistical significance $[F(1, 11) = -4.27; p = .001; \eta 2p = .624]$. *Post-hoc* pair-wise comparisons showed differences in RTs between all grouping conditions, with faster RTs in the cooperative condition followed by the single and competitive conditions (see Figure 3-right and Table 1 bottom row).

Table 1. Experiment 1. Mean response times as a function of grouping condition, for both relative and absolute target positions

Target position	Grouping condition				
	Single	Coop.	Comp.	Fac.	Interf.
Relative	2995 (483)	3077 (472)	3195 (518)	82 (126)	200 (154)
Absolute	3256 (551)	2812 (411)	3456 (597)	-444 (184)	200 (202)

Single: similarity only condition; Coop.: cooperative condition; Comp.: competitive condition; Fac.: Coop. RTs – Single RTs; Interf.: Comp. RTs – Single RTs

A 2-way repeated measures ANOVA conducted on accuracy (error rates) showed that neither the main effects nor the interaction reached statistical significance (all ps > 0.05). The mean accuracy of the task was 94%.

2.3.2. EEG results: IC-cluster Event-Related Spectral Perturbations

After pre-processing the EEG data, the remaining ICs (139) were grouped into 8 clusters according to their dipole locations, scalp maps, spectral power and ERSP activity (weighted by a factor of 10, 5, 1 and 3 respectively). In addition, and given that no significant interaction between grouping conditions and target position was found, we collapsed the data from all the different target positions to increase

the statistical power. Two participants were removed from the EEG analyses due to the noisy data. Thus, all the EEG analyses were conducted on the remaining 19 participants. Five clusters were selected to enter the statistical analyses following the criteria specified in section 2.2.2: Left and right sensorimotor, right prefrontal, right parietal and left occipital. The scalp maps, dipole source localizations and power spectra of the selected IC clusters are plotted in Figure 4.

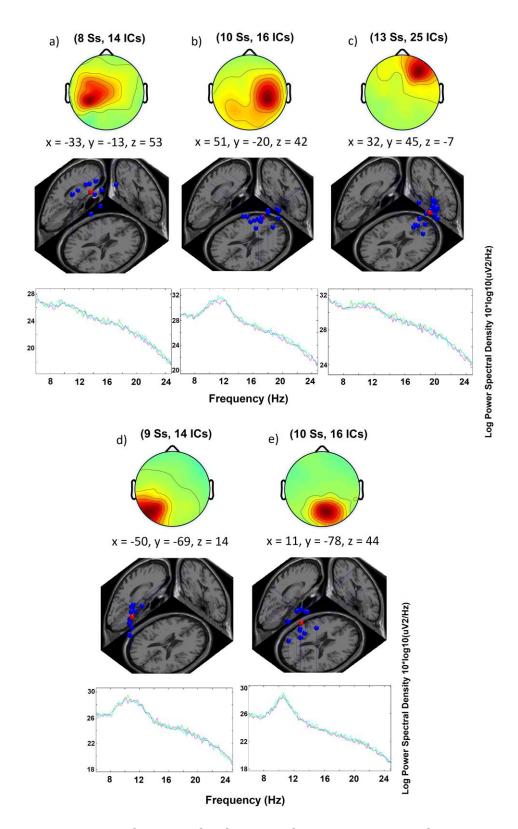


Figure 4. Average scalp maps, dipole source location in average brain images (the red dot represents the cluster centroid), Talairach coordinates and power spectra of 5 IC clusters from 19 subjects. (A) Left sensorimotor (n=14); (B) right sensorimotor (n=16); (C) right pre-frontal (n=25); (D) left occipital (n=14) and (E) right parietal (n=16).

To analyze differences in oscillatory brain activity between grouping conditions, ERSPs were computed and plotted under all experimental conditions along with significant differences between them (see Figure 5).

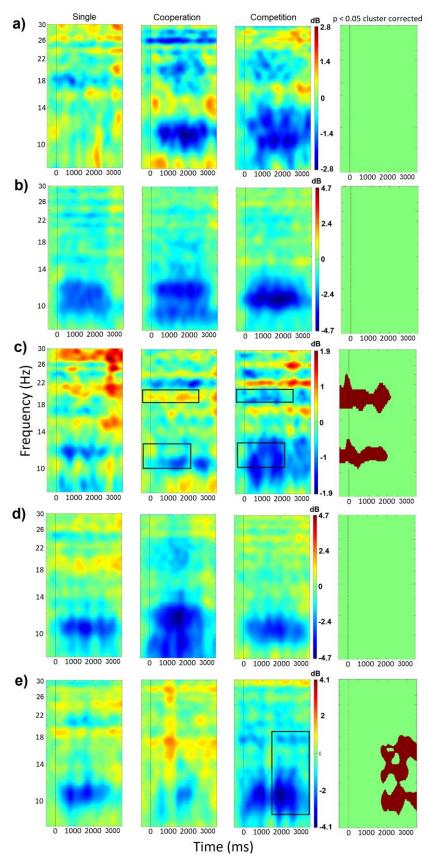


Figure 5. Average event-related spectral perturbations (ERSP) of the five IC clusters selected for further analysis in the three grouping conditions of Experiment 1. From top to bottom: left sensorimotor, right prefrontal, left occipital and right parietal.

Figure 5c shows the oscillatory brain activity of a right prefrontal IC cluster (Brodmann area 10, right dorsolateral pre-fontal cortex). The analysis of the ERSP showed significant differences in alpha-band (10-12 Hz) event-related desynchronization (ERD) between conditions. Post-hoc comparisons showed that this ERD was significantly more pronounced in the competitive condition compared with the cooperative condition throughout the first 2000 ms of the epoch. Additionally, we found beta-band ERD around 20 Hz. Post-hoc comparisons indicated that it was more pronounced during the first 2000 ms of the competitive condition than in the other grouping conditions.

ERSP from a right parietal IC cluster (Brodmann area 7, somatosensory association cortex) is plotted in Figure 5e. ERSP analyses showed significant alpha (10-12 Hz) and beta (15-25 Hz) band ERD differences between grouping conditions. Post-hoc comparisons indicated that this ERD was more pronounced in the competition condition relative to cooperative condition throughout the 1500-3500 ms interval. Finally, Figures 5a, 5b and 5d display the ERSP of the left sensorimotor (Brodmann areas 4-6, motor and premotor cortex), right sensorimotor (Brodmann areas 1-2-3, primary somatosensory cortex) and left occipital (Brodmann area 19, associative visual cortex) IC clusters respectively. All three IC clusters showed a marked alphaband (10-12 Hz) ERD that began within the first 500 ms of the epoch, peaked in the interval between 1500-2000 ms, and started to re-synchronize within the last 1000 ms of the epoch. Beta-band ERD (18-20 Hz) was also evident in all three IC clusters, especially in the left sensorimotor one (see Figure 5a), but its duration and intensity was lower than the alpha-band desynchronization. Notably, in the clusters and conditions in which the beta band was more pronounced, beta-band ERD began about 500 ms after the onset of the haptic exploration and started to

resynchronize after the first 2000 ms of the epoch. No statistically significant differences between grouping conditions appeared in any of the three IC clusters (left and right sensorimotor, left occipital).

3. Experiment 2

The results of Experiment 1 indicate that the conjoined effect of proximity grouping exerts an influence on performance of a task in which target discrimination depends on grouping by texture similarity. Specifically, the task was facilitated when proximity grouped the haptic pattern in the same way as texture similarity (cooperation condition), while performance was hindered when proximity grouped the pattern in opposite different way (competitive condition). The ICA analysis and IC clustering also revealed the activation of a widespread network of bilateral sensorimotor areas, along with right parietal, right prefrontal and left occipital cortices. In addition, the ERSP analysis showed greater activation in both the pre-frontal and parietal clusters, as reflected by the stronger alpha- and beta-band ERD in the competition condition. In Experiment 2, we examined the influence of grouping by texture similarity in a task in which targets were defined by means of spatial proximity grouping. Here, we employed a variant of the discrimination task in which participants were presented with a row of 6 to 8 elements that formed two different cohorts (left/right) based on their spatial proximity. Participants had to indicate which side of the haptic display (cohorts grouped by spatial proximity) had more elements, or not respond if the number of elements was the same (catch trials). In this case, texture similarity facilitates (cooperation condition) or hinders (competition condition) the proximity-based task.

3.1. Method

3.1.1. Participants

A new group of 23 students (6 males; age range: 19-50, mean age = 30.55, SD = 7.73) from the Universidad Nacional de Educación a Distancia (UNED) participated in Experiment 2. All of them reported being right-handed, had normal tactile perception and were naïve to the purpose of the experiment. Before the start of the experiment they completed the same handedness inventory and informed consent form as in Experiment 1.

3.1.2. Apparatus and stimuli

The device and the haptic stimuli were the same as in Experiment 1. The stimuli were arranged in a row of 6 to 8 elements with three different configurations: (1) In the cooperative condition, each cohort was defined by spatial proximity (6 mm within cohorts; 24 mm between cohorts), and all its elements had the same texture, but the texture of each cohort was different; (2) In the competitive condition, all the cylinders of the cohort with the largest number of elements had the same texture, except the last one (the nearest to the opposite cohort), which had the same texture as the opposite cohort; (3) Finally, single (proximity acting alone) stimuli were those in which the texture of the two cohorts alternated, without any explicit texture similarity grouping. Figure 6 shows a list of the different displays used in Experiment 2.

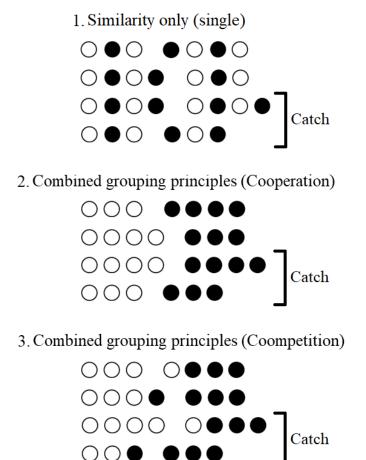


Figure 6. Representation of all the experimental conditions used in Experiment 2: (1) proximity acting alone, (2) cooperation between grouping principles, and (3) competition between grouping principles. The bottom two rows of each condition represent the catch trials.

3.1.3. Design and procedure

We employed a unifactorial within-subjects design with 3 grouping conditions (cooperative, competitive, neutral). As in Experiment 1, the dependent variables were RT and accuracy. Participants indicated as fast and as accurately as possible which of the two cohorts had the most elements. Participants explored the row of elements sequentially with the index and middle fingers of the right hand and responded by pressing one of two foot pedals (one for the "left" and the other for the "right" cohort). In addition, to avoid the possibility of identifying the largest cohort without exploring the whole haptic pattern, catch trials were added, in

which the number of elements was the same in both cohorts; for these trials, participants were instructed to make no response (see Figure 6). The total number of trials (120: 96 + 24 catch trials) was conducted in a single block lasting approximately 40-50 minutes. The rest of the procedure was the same as the one described in Experiment 1 (see paragraph 2.1.3).

3.1.4. EEG acquisition and pre-processing

EEG acquisition and offline pre-processing followed the same procedure as in Experiment 1 (see paragraph 2.1.4). The mean number of artifact-free epochs per participant was 71 (Min/Max: 55-79).

3.2. Data analysis

3.2.1. Behavioral data

We conducted two separate unifactorial repeated measures ANOVAs with 3 grouping conditions (cooperative, competitive, single) on RTs from trials followed by correct responses (16.66% of trials rejected) and accuracy (error rates). All the statistical tests were Bonferroni corrected.

In addition, to examine the compatibility of the data from both Experiments with an additive model of the interaction between grouping effects, we transformed the RT data to obtain normalized effect sizes, employing a method similar to the one used by Kubovy and van den Berg (2008). To this end, we first computed a differential variable I by transforming the raw RTs as follows: I = single condition – conjoined condition (competitive or cooperative). Positive scores indicate the facilitation (ms) of the non-relevant grouping cue, whereas negative scores indicate the interference of the non-relevant cue. The differential scores of Experiments 1 and 2 are summarized in Tables 1 and 2 respectively. After that, I was normalized using the effect size D (D = I/Standard error of I). The D values

were then adjusted to fall between the -1/+1 interval by assuming the highest D value as 1 (or -1) in the normalized scale and computing the remaining normalized effect sizes as the ratio between the observed D and the highest D (D / highest D value observed). The 0 value represents the scores for single conditions.

3.2.2. Independent component analysis (ICA) and component clustering

ICA analysis and component clustering followed the same procedure as in

Experiment 1 (see paragraph 2.2.2)

3.2.3. Time/frequency analysis of event-related spectral perturbations (ERSP) As in Experiment 1, event-related spectral changes in power spectrum (ERSP) for each IC cluster were computed over the entire epoch length (-1000 – 4000 ms) in each experimental condition (Makeig, 1993). The details of ERSP computing were the same as in Experiment 1(see paragraph 2.2.3).

Statistical analyses of EEG recordings were conducted following the same guidelines outlined for Experiment 1 (see paragraph 2.2.4).

3.3. Results

3.3.1. Behavioral results

Behavioral data from Experiment 2 were analyzed using a unifactorial repeated measures ANOVA on both response times and task accuracy (the main results are summarized in Figure 7 and Table 2).

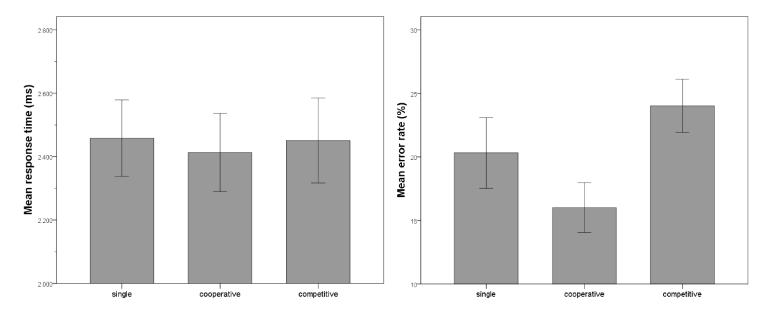


Figure 7. Left: Mean RT (ms) for the three different grouping conditions. Right: Mean error rates (%) for the three grouping conditions (the bars represent ±1 SE).

Table 2. Experiment 2. Mean response times as a function of grouping condition.

Grouping condition					
Single	Coop.	Comp.	Fac.	Interf.	
2458 (579)	2413 (592)	2451 (643)	-46 (112)	-7 (135)	

The results of the ANOVA performed on RT data show no significant effects of grouping condition (all ps > .05). The ANOVA conducted on accuracy (error rates) shows that the main effect of grouping was significant [F (2, 21) = 7.22; p = .004; $\eta 2p$ = 0.407]. Pairwise comparisons indicate that the number of errors in the competitive condition was greater than in the cooperative condition (p = .003). No other effects reached statistical significance (all ps > .05).

3.3.2. Compatibility with an additive model of grouping effects

The results obtained from the normalization of the effect sizes in Experiments 1 and 2 showed that both cooperative conditions fall above the single condition, indicating larger facilitation effects when proximity was the non-relevant cue (Experiment 1). In the competitive conditions, the normalized size effects were

below the single condition and were only evident when proximity was the non-relevant cue. This result suggests that interference effects only appeared in Experiment 1, when proximity was the interfering cue. The normalized effect sizes are summarized in Figure 8 and the inferences about additivity are listed in Table 3.

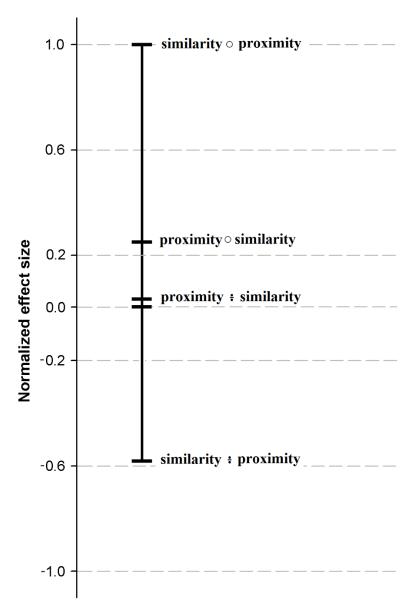


Figure 8. Normalized effect sizes used to examine the additivity of the data from Experiment 2. Cooperation between principles is identified by (o) and competition by (÷). The grouping cue on the left is the task-relevant one, and the one on the right non-relevant (interfering). Positive scores indicate facilitation and negative scores interference.

Table 3. Inferences about the compatibility of the data from Experiments 1 and 2

with additivity effects of grouping

with additivit	y effects of grouping	Relation to additivity		
Data	Inference	Compatible	Not incompatible	Incompatible
$D\left(s \circ p\right) > D\left(s\right)$	The O combination of s and p is stronger than s	✓		
$D\left(p\mid 0\mid s\right)>D\left(p\right)$	The O combination of p and s is stronger than p	✓		
$D\left(s \div p\right) < D\left(s\right)$	The \div combination of p and s is not stronger than p	✓		
$D\left(p \div s\right) < D\left(p\right)$	The \div combination of p and s is not stronger than s		✓	
$D(p \circ s) > D(p \div s)$	The O combination of p and s is stronger than the \div combination of p and s	✓		
$D(s \cap p) > D(s \div p)$	The O combination of s and p is stronger than the \div combination of s and p	✓		
$D(p \circ s) > D(p) > D(p \div s)$	The O combination of p and s is stronger than p and the \div combination of p and s		✓	
$D(s \cap p) > D(s) > D(s \div p)$	The O combination of s and p is stronger than s and the \div combination of s and p	·		

D represents the normalized measure of effect sizes; p, proximity; s, similarity; o, cooperation; \div , competition. The first grouping cue within parentheses is the task-relevant cue, and the second is the non-relevant (interfering) one.

3.3.3. EEG results: IC-cluster Event-Related Spectral Perturbations

After the pre-processing of the EEG data, the 169 remaining ICs in Experiment 2 were grouped into 8 clusters according to their dipole locations, scalp maps, spectral power and ERSP activity. One participant was removed from the EEG analyses due to the noisy EEG data, so all the EEG analyses were conducted on the remaining 22 participants. According to the criteria established, statistical analysis was conducted on five IC clusters, whose overall locations were similar to those

found in Experiment 1: left and right sensorimotor, right prefrontal, right parietal and left occipital. The features of the selected IC clusters are plotted in Figure 9.

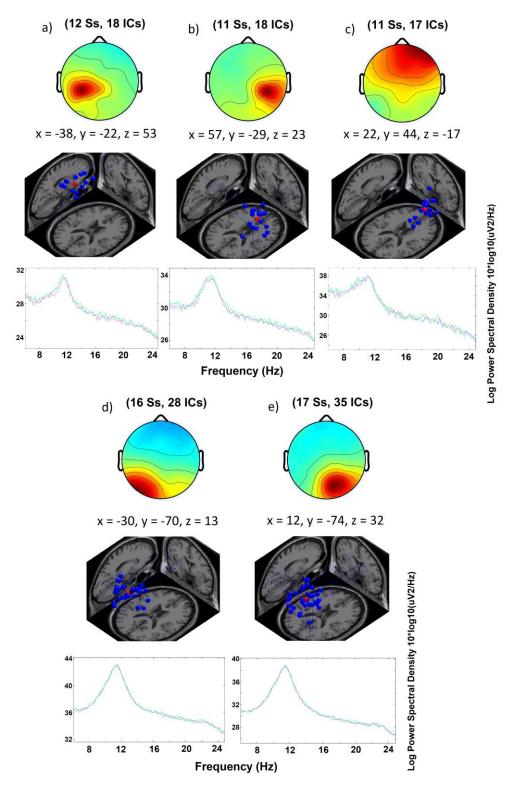


Figure 9. Average scalp maps, dipole source location in average brain images (the red dot represents the cluster centroid), Talairach coordinates and power spectra of 5 IC clusters from 22 subjects in Experiment 2. (A) Left sensorimotor (n=18); (B) right sensorimotor (n=18); (C) right pre-frontal (n=17); (D) left occipital (n=28); (E) right parietal (n=35).

Figures 10a and 10b show the ERSPs of left (Brodmann areas 4-6, right primary motor and pre-motor cortices) and right (Brodmann area 40, supramarginal gyrus) sensorimotor IC clusters. Both clusters showed a strong alpha-band ERD, especially in the 10-12 Hz range. The alpha ERD began immediately after the onset of the haptic exploration in both clusters, but in the left sensorimotor cluster the resynchronization of the alpha band started earlier (around 3000 ms) than in the right sensorimotor cluster, in which alpha-band ERD seemed to last throughout the entire epoch. Beta-band ERD (18-22 Hz) was also evident in both IC clusters, but its duration and intensity was lower than the alpha-band ERD. In addition, beta-band activity in the left sensorimotor cluster showed an event-related synchronization (ERS) following the ERD in the last 1000 ms of the epoch. No statistically significant differences between conditions arose in either IC cluster.

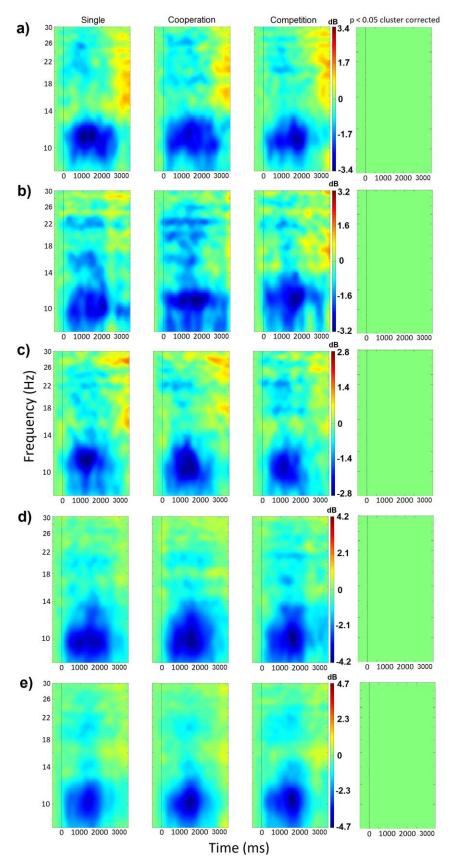


Figure 10. Average event-related spectral perturbations (ERSP) of the five IC clusters selected for further analysis in the three grouping conditions of Experiment 2. From top to bottom: left sensorimotor, right prefrontal, left occipital and right parietal.

The results of the event related spectral activity from the right frontal (Brodmann area 10, right dorsolateral pre-fontal cortex) and right parietal (Brodmann area 7, somatosensory association cortex) IC clusters are plotted in Figures 10c and 10e, respectively. The two clusters showed a similar alpha-band ERD from the beginning of the task period, centered in the 10-12 Hz range and peaking around 1500 ms. The alpha band started to resynchronize approximately in the 2000-2500 ms time window. Beta-band activity followed a similar pattern in the two clusters, with an intensity peak that coincided with the intensity peak of the alpha band. No statistical differences were found between conditions.

Finally, Figure 10d shows the ERSP activity of the left occipital IC cluster found in Experiment 2 (Brodmann area 19, associative visual cortex). As in the previous IC clusters, there was a strong alpha-band ERD centered around 10 Hz that peaked around 1500 ms and resynchronized about 2000 ms after the start of the task period. Beta-band ERD, on the other hand, was located in the 20-22 Hz range and peaked at the same time as the alpha-band ERD. No significant differences were found between grouping conditions.

4. General discussion

The aim of the current study was to examine the interaction effects and dominance dynamics between grouping principles in touch, along with their neural correlates. This work was motivated by the scarcity of research addressing the topic in the haptic modality. To the best of our knowledge, this is the first study to investigate the interactions between grouping principles in touch and the brain activity that underlies the perceptual grouping processes when grouping cues interact in the haptic modality.

Four main conclusions can be drawn from this haptic study: (1) proximity dominated the perceptual grouping process when it acted conjoined with texture similarity; (2) the results are compatible with an additive model of the interaction between grouping principles; (3) ICA revealed the involvement of a widespread network of ipsi- and contra-lateral sensorimotor, ipsilateral (right) prefrontal and parietal, and contralateral (left) occipital brain areas in both experiments; and (4) ERSP analyses indicated a greater activation of right dorsolateral pre-frontal and parietal IC clusters in the competitive condition in Experiment 1, which in turn could be related to the dominance and more intense interference of proximity over similarity cues. These results and their implications are discussed in the following sections.

4.1. Dominance dynamics and additive effects of interactions between grouping principles in touch

In Experiment 1, participants responded faster when the grouping cues cooperated to group the stimuli in the same way. By contrast, RTs were slower when the two grouping cues competed so that proximity tended to group the target with the distractors. On the other hand, in Experiment 2 the non-relevant cue (texture similarity) did not affect RTs in either the competitive or the cooperative condition, although participants made more errors when the two principles where conjoined in competition. In addition, comparison of the overall RTs between experiments indicates that participants responded faster when targets were grouped by proximity (Experiment 2) than by similarity (Experiment 1). Finally, the analysis of the normalized effect sizes supports the RT and accuracy data. The effect sizes of the conjoined conditions (competition and cooperation) were much larger when the non-relevant cue was proximity (Experiment 1) than when it was

texture similarity (Experiment 2). Thus, this pattern of results supports our hypothesis regarding the dominance of proximity grouping when the two principles act together, because: (1) participants' responses were faster and more accurate when targets were grouped by proximity; (2) proximity grouping was less interfered by the competitive presence of texture similarity; and (3) responses to similarity grouped targets were facilitated by the cooperative presence of proximity cues, but not vice versa. Importantly, the dominance of proximity grouping occurred even though the phenomenological strength of the two grouping cues was equated.

Our haptic results agree with previous findings in vision using explicit and non-explicit attentional psychophysical tasks (Luna et al, 2016; Palmer & Beck, 2007). In those visual studies, responses were slowed down by the non-attended/non-relevant grouping cues when grouping principles were conjoined in competition and speeded up when the two principles cooperated, compared to the condition when one principle acted alone. Interestingly, the specific cues that dominate the perceptual scene seem to differ between modalities. Specifically, Quinlan and Wilton (1998) found no dominance of proximity when it was pitted against color and shape similarity (see also, Luna et al., 2016).

At least two studies have compared these two grouping principles in touch. First, Chang et al. (2007b) investigated whether people grouped visual and haptic displays in the same manner when proximity and color/texture similarity were used as grouping cues. Their results indicate that when an unequal distance was perceived between the individual elements, the participants tended to group them using spatial proximity rather than texture similarity, a finding that matches the proximity dominance found in the present study. Furthermore, a previous study

(Prieto et al., 2014) showed faster and more accurate responses to proximity-grouped stimuli in a speeded haptic task in which participants had to detect the orientation of haptic patterns formed by either proximity or texture similarity.

Moreover, we found that most of our data (except in the competition condition, Exp.2) fall into an impressively regular pattern, in which the single (acting alone) grouping principles fall between the two conjoining (competitive/cooperative) conditions as shown in vision (Kubovy & van den Berg, 2008). This overall pattern allows us to infer that the interaction effects between proximity and texture similarity in touch can be accounted for by an additive model of grouping effects. However, these results cannot be taken as definitive, as different tasks, grouping cues, and combinations of grouping strengths need to be considered to draw solid and generalizable conclusions about the additivity of perceptual grouping in touch.

4.2. Independent Component Analysis (ICA) and Event-Related Spectral Perturbations (ERSP)

The transient ERSP in alpha and beta spectral power of ICA-decomposed EEGs shows that the two experiments involved activation of similar brain areas, as revealed by the spectral activity of the clusters obtained after ICA decomposition, and the localization of the equivalent dipoles of each cluster (Figures 4 and 9). According to the hypotheses of the study, these areas include left and right sensorimotor μ clusters. The bilateral localization around the central sulcus, spreading across the motor, pre-motor and somatosensory cortices is consistent with the commonly reported sources of this rhythm (Pineda, 2005) and its implication in haptic tasks (Lin et al., 2012). The brain areas involved also include right parietal and pre-frontal IC clusters. The first area has been related to diverse functions in haptic perception such as: goal-directed finger movements in object

exploration (Binkofski et al., 1999), length discrimination (Bodegård et al., 2001), and shape representation (Reed, Caselli, & Farah, 1996). The right pre-frontal cortex, on the other hand, has been associated with a great number of high order and executive functions, including: encoding of non-verbal material (Kelley et al., 1998), active maintenance of somatosensory information (Fletcher & Henson, 2001), response selection (Rowe, Toni, Josephs, Frackowiak, & Passingham, 2000), and the organization of the entire process (exploration-discrimination-response selection) of the task (Stoeckel et al., 2003). More interestingly, the conjoined activation of frontal (including pre-motor) and parietal areas is thought to be implicated in the processing and short-term storage and discrimination of stimuli (Stoeckel et al., 2003). Finally, the activity of the left occipital IC cluster found in both experiments might indicate the activation of visual areas. This contribution of visual areas has been reported in other haptic studies, especially in object recognition (Sathian, 2005). As the active sites found in IC-cluster analysis are known to play an important role in haptic perception, the findings support the detailed analysis of the real-time activity within these clusters. In the following sections we will discuss each of them in turn.

4.2.1. Left and right sensorimotor clusters

The present study clearly shows the engagement of left ipsi- and contra-lateral sensorimotor IC clusters in a haptic exploration task. The ERSP analysis for right and left sensorimotor clusters in Experiments 1 and 2 showed alpha- (10-12 Hz) and beta- (18-22 Hz) band event-related desynchronization (ERD) in both IC clusters. Given that alpha-band desynchronization has been linked to high excitability and increased brain activity (Klimesch et al., 2007), the ERD found in the left (contralateral) sensorimotor cluster, involving areas surrounding the

central sulcus, is not surprising. In this way, the alpha ERD may be related to movement organization, voluntary hand and finger movements during the task (primary motor cortex), somatosensory perception, finger proprioception, and localization of touch (primary somatosensory cortex). This is in accordance with earlier studies that found similar activity during tactile object exploration of macro-geometric objects using fMRI. In particular, Boecker et al. (1995) found similar bilateral activation of the primary sensorimotor cortex (M1, S1), supplementary motor areas (SMA) and pre-motor areas (PMA) across participants. A similar but less pronounced ERD/ERS pattern was explicit in the beta band. Even though its functional significance is not as well understood as the alpha band, the desynchronization of beta rhythms within the sensorimotor cortex in response to external stimuli has usually been related to sensory processing, motor learning and motor skills (Sochůrková, Rektor, Jurák, & Stančák, 2006). In particular, Gaetz and Cheyne (2006), using transient brush stimuli, found beta-band ERD in sensory cortical areas (S1) that was organized somatotopically. Moreover, Lin et al. (2012), using a visuomotor tracking task, found stronger beta-band suppression in epochs with haptic feedback due to the increased sensory processing and motor demands, in a contralateral sensorimotor IC cluster of similar characteristics and localization as the one found in our study. Taken together, the results agree with previous EEG and fMRI studies that linked the increased bilateral activity in sensory and motor areas (especially in alpha and beta bands as the components of the μ rhythm) with the performance of voluntary movements, and the acquisition and processing of tactile information through the fingertips. Finally, the lack of significant differences between grouping conditions in Experiments 1 and 2 was also expected, given that

the haptic exploratory activity and the sensory processing demands were almost identical in the different experimental conditions.

4.2.2. Right parietal and pre-frontal clusters

Besides the recruitment of sensorimotor areas, the analysis of the oscillatory brain activity (Experiments 1 and 2) revealed the activation of right (ipsilateral) parietal and pre-frontal IC clusters. Both clusters showed increased alpha- and beta-band ERD during the task period that peaked around 10-12 and 18-22 Hz respectively and began to resynchronize approximately at the start of the behavioral response, especially in Experiment 2. The increased activity within the right parietal cortex has been associated with several different cognitive processes, particularly in the spatial domain. Previous studies also reported that the right parietal lobe plays an important role in the integration of spatial information and sensorimotor behavior, especially when the movements are guided by external haptic feedback (Classen et al., 1998). On the other hand, Roland, O'Sullivan and Kawashima (1998) found that different areas of the parietal lobe, namely the anterior intraparietal sulcus (IPA) and the lateral parietal operculum (LPO), were involved in the discrimination of the macro- (shape and length) and micro-geometric (rough) properties of the tactile objects, respectively. Activity within the parietal lobe has also been associated with attention and short-term storage of somatosensory information, particularly in the context of its association with the pre-frontal cortex (Smith & Jonides, 1997). In this connection, the increased activity of the right dorsolateral prefrontal cortex has also been linked to the manipulation of non-verbal information during working memory tasks (Rowe et al., 2000). The strong connections between the parietal and the prefrontal cortex would be responsible for the transfer from unimodal specific areas to the areas where information is

manipulated and updated online (Petrides & Pandya, 1984). Interestingly, this fronto-parietal circuit also seems to play a crucial role in tactile object discrimination (Stoeckel et al., 2003). Taking this evidence into account, the engagement of the right parietal and prefrontal areas in both Experiments might be related to the need to integrate the micro- (roughness) and macro-geometric (spatial proximity and total length) features of the haptic patterns into a unified percept. According to this view, the conjoined activity of the parietal and prefrontal cortex would be necessary to integrate or group the disjointed information of each individual item, to maintain this information in working memory, and to update/manipulate it as the haptic exploration continues. The integrated/grouped information would then be used to discriminate between the different possible stimulus configurations and make a decision about the appropriate response according to the task goals. This could also explain the more intense ERD in alpha and beta bands in the competitive condition in Experiment 1. The enhanced brain activity would result from the greater cognitive demands in the grouping process when participants tried to integrate incongruent cues into a coherent and stable percept. The fact that both clusters showed significant differences between conditions in sequential time windows suggests the joint action of the two areas within a parieto-frontal integrated circuit of tactile discrimination (Stoeckel et al., 2003).

4.2.3. Left occipital cluster

The analysis of the activity in the left occipital IC cluster indicates the engagement of the occipital visual areas in our haptic grouping tasks. In both experiments, analysis of the ERSP shows a clear ERD extended over all the task period in the alpha band (10-12 Hz), accompanied by a less pronounced and lasting beta-band

ERD (20-22 Hz). There is strong evidence suggesting that tactile perception evokes activity within visual cortical areas, particularly the parieto-occipital region (POC) and lateral occipital complex (LOC). Several studies reported this evidence in a number of different tasks and cognitive processes, including tactile discrimination of grating orientation (Zhang et al., 2005), perception of two-dimensional patterns and three-dimensional objects (Prather, Votaw, & Sathian, 2004), shape processing (Snow et al., 2014), and object recognition (Strother, Zhou, Vilis, & Snow, 2016). Interestingly, two different studies have found increased activity within the left lateral occipital complex (LOC) in tasks that require either the tactile discrimination of the orientation of gratings (Zangaladze et al., 1999) or the tactile discrimination of macrospatial features of the stimuli (Stoesz et al., 2003). By contrast, they did not find any activity within the LOC when the tasks involved the detection of microspatial features (detecting a gap) or texture discrimination. Given that our tasks relied specifically on texture and gap (proximity) features, our findings of the engagement of the occipital cortex, especially in extra-striate areas that overlap with the areas included in the LOC (Grill-Spector, Kourtzi, & Kanwisher, 2001), are somewhat surprising. One possible explanation is that discrimination between textures and/or different spatial proximities was not the primary goal of our grouping tasks. Our participants performed indirect tasks in which they were not aware of the relevance of the grouping cues. Consequently, the engagement of visual areas could result from the need to form a representation of the haptic stimulus after the integration of low-level features. In fact, some studies have emphasized the role of visual imagery in the haptic perception of orientation, shape and size (Zangaladze et al., 1999). In addition, Strother et al. (2016) found that activation of visual areas was contralateral to the hand used and

not dependent on the side of the presentation, which is in line with the left occipital activity obtained in the present study. Another possible explanation is that activity in visual areas does not reflect the conversion of the haptic information into visual imagery, but some kind of multisensory representation of information. This possibility has already been contemplated in studies that found different occipital activation patterns for spatial and non-spatial tasks (Prather et al., 2004) and different reference frames for visual and haptic tasks (Strother et al., 2016). However, the present study cannot disentangle the two explanations, as it did not vary the type of task (spatial *vs* non-spatial) or the location of the haptic stimuli with respect to the body midline. Finally, the absence of statistical differences between grouping conditions was expected, given that the low-level features of the haptic stimuli were the same across the different experimental conditions.

5. Shortcomings, limitations and future directions

The procedure used in the present study could be a useful method for investigating in greater depth the perceptual organization processes in a long-neglected sensory modality. Future work should extend the grouping principles under investigation and introduce each grouping principle as a multilevel factor, to draw solid conclusions about the dominance dynamics between different grouping principles and the additivity of the grouping effects in touch. In addition, adapting other tasks to the haptic modality (phenomenologically and/or psychophysically directed attention tasks) would help overcome the limitations of the paradigm used here. In particular, it is not possible with the present approach to obtain individual

estimates of grouping strength, or to evaluate the effect of attentional manipulations on the grouping process.

Regarding the analysis of the brain activity, ICA clustering made it possible to separate and identify independent brain sources of activity implicated in the grouping process. However, future research should address the coupling between the different regions of the cortex to establish the functional relationship between those areas. At least two different measures could be useful for this purpose. First, event-related coherence (ERCOH), which determines the degree of synchronization between different IC clusters at different frequencies and latencies (Lin et al., 2012). Secondly, the use of Granger-causality models to analyze the information flow and infer the causal dependency between different sources of electrophysiological activity (Mullen, Delorme, Kothe, & Makeig, 2010). These two methods could constitute an important tool to understand how the different brain areas involved in the haptic grouping process cooperate, and the functional role played by each. Another important venue for future research would be to study the cross-modal effects between sensory modalities in perceptual grouping and their neural correlates, to investigate whether perceptual grouping constitutes a multimodal process shared between sensory modalities, or, on the contrary, whether it is specific to each perceptual modality. To conclude, it is worth noting the potential practical applications of a better knowledge of how the tactile perceptual scene is organized into meaningful objects in several areas; for example, to design visuo-tactile interfaces or develop tactile resources for visually impaired people.

6. Acknowledgments

A Doctoral Fellowship from MECD granted to AP (FPU13/05914) supported this work, and grants from the Spanish Government (PSI2013-41409-R and PSI2016-80337-R) to SB and from the Universidad Nacional de Educación a Distancia (2014-028-UNED-PROY) awarded to JM.

Haptic Perceptual Grouping: Behavioral and Neurophysiological Correlates

CHAPTER 9: GENERAL CONCLUSIONS

Haptic Perceptual Grouping: Behavioral and Neurophysiological Correlates

This Thesis had three main objectives (Chapter 4). The first goal was to study the time course and dominance dynamics of proximity and texture-similarity in the haptic modality. The second goal was to study the interactions between these grouping principles and the compatibility with an additive model of grouping effects. Finally, the third goal was to analyze the neurophysiological correlates of haptic grouping and the interactions between grouping principles. To achieve these objectives, we conducted six experiments in which we adapted to the haptic modality some of the most widely employed tasks in the perceptual grouping research in other sensory modalities. In the following paragraphs, we will discuss the main results of this investigation and their implications for the objectives outlined above.

To address the **dominance dynamics** of proximity and texture-similarity grouping principles in touch, we assumed the classic rules of processing dominance in the perception literature (Navon, 1977; Pomerantz, 1983; Ward, 1983), which establish that the grouping principle that produces faster and/or more accurate responses is less interfered by the (competitive) presence of other grouping cues and leads to greater improvement of the responses to the other cue when both are presented in cooperation, will dominate the perceptual organization of the scene. Additionally, and in agreement with previous evidence (Chang et al., 2007b; Han et al., 2001), we hypothesized that proximity grouping will dominate the haptic grouping. According to these criteria, our results supported our initial hypothesis regarding the dominance of proximity grouping at least for three different reasons:

1. The first reason is the significantly shorter RTs for groups formed by proximity found in Experiments 1, 2, 4 and in the comparison between

Experiments 5 and 6. Interestingly, these results have been found in all the three different tasks employed in our study. The first task was an orientation (vertical/horizontal) detection task used in Experiments 1 and 2. In this task, attention was directed to the grouping itself and grouping cues were always presented in isolation. The second task was a left/right orientation task (Experiment 4). In this task, attention was directed to a specific grouping principle and cues were presented both in isolation or conjoined in cooperation or competition. The last were the feature discrimination tasks used in Experiments 5 and 6. In this case, the grouping cues were also presented conjoined or in isolation and neither required explicit attention to the grouping cues nor any knowledge about the purpose of the task.

- 2. The second reason was that responses to proximity-grouped elements were less interfered both in terms of RTs and error rates by the competitive presence of similarity cues than on the contrary (Experiments 4, 5 and 6). Moreover, responses to similarity-grouped targets were facilitated under some conditions (Experiment 5, non-directed attention) by the cooperative presence of proximity cues, but the contrary did not occur. Thus, convergent evidence was obtained on the dominance of grouping by proximity from directed and non-directed attention tasks.
- 3. Finally, phenomenological responses (Experiment 3) indicated that even though the perceived phenomenological strength of both grouping principles was similar, when the cues were conjoined in competition, participants tended to group the haptic stimulus by proximity, as indicated by the global ratings and the proportion of participants who grouped the patterns by proximity and similarity (14 vs 5, respectively).

A tentative explanation of the dominance of proximity grouping is outlined in the discussion of Experiments 1 and 2. According to this view, grouping by proximity produces faster responses and dominates the haptic grouping because it could be considered a holistic/configural property that relies on the relationship of the individual components. These features describe a relation between the elements of the stimulus rather than informing about a feature of the element itself. This means that proximity gives information about the organization of the global pattern, without the need to identify the particular features of each single element (Kimchi, 1994; Kimchi & Bloch, 1998). On the other hand, texture could be considered a component feature that requires the identification of the specific value of the feature in each element prior to integrating this information into a whole percept. This fact ultimately leads to the faster identification of the patterns grouped by proximity. In other words, when the haptic stimuli are grouped by proximity, participants could use the distinct spatial gaps in the array to organize and identify the global pattern without the need to identify and integrate the local characteristics of each element. In contrast, the stimuli grouped by similarity require the identification of the local component properties of each single element (whether the texture is rough or smooth) as well as the integration of this information into a global organization to come up with an answer. This explanation is also supported by the results of Experiment 1 regarding the effect of the vertical/horizontal orientation of the array. In this experiment, the well-known advantage in the detection of bilaterally symmetric patterns along the body midline axis (Ballesteros et al., 1997, 1998; Ballesteros & Reales, 2004) only appeared when the stimuli were grouped by proximity, an expected result given that this detection is based on holistic/configural properties (Kimchi, 1994). Finally, the

faster detection of holistic properties would also be responsible for the greater interference/facilitation effects found when grouping principles act conjoined within the same stimulus. In this case, if proximity cues are available earlier, they might influence the processing of similarity-based targets but not vice versa.

The study of the **interactions between those grouping principles and the compatibility with an additive model** of grouping effects was addressed in Experiments 3 to 6. We based our predictions about additivity in the model proposed by Kubovy and van den Berg (2008). This model offers predictions that can be tested under experimental conditions. The model is grounded on two simple assumptions. The first is that additivity can be inferred if the grouping strength of grouping principles acting in cooperation is greater than the strength of each of them acting alone. The second assumption is that the strength of grouping principles in a competitive configuration is weaker than either principle acting alone. According to results obtained, our data seems to be highly compatible with an additive model of grouping effects when more than one principle is present within the same stimulus. This conclusion is supported by two different kinds of evidences:

1. The subjective ratings of grouping strength obtained in Experiment 3 in a phenomenological task. The ratings were consistently higher when both grouping principles cooperated, and lower when the grouping principles competed, as predicted by the additive model. Moreover, acting alone conditions consistently fell between the cooperative and the competitive conditions and did not differ between them. Interestingly, the ratings of the participants were remarkably consistent (e.g., if one participant rated proximity as stronger than similarity in the acting alone conditions, his/her

rating in the competitive condition usually reflected the proximity dominance and vice versa).

2. The analysis of the normalized effect sizes in the phenomenological and psychophysical directed and non-directed attention tasks (Experiments 3, 4, 5 and 6). To obtain a common measure of the fit of the data to an additive model that could be compared across the experiments, we computed a normalized measure of the effect sizes, following the procedure established by Kubovy and van den Berg (2008). This normalization process yielded an impressive regular pattern in all three tasks. Particularly, acting alone conditions always fell between the competitive and cooperative conditions, thus supporting the hypothesis derived from the predictions of the model.

Despite the evidence supporting the compatibility of the interactions between grouping principles with an additive model, and in order to draw solid conclusions on the additivity of the haptic perceptual grouping, it is necessary to extend the strategies employed and the grouping principles under investigation. Moreover, it is necessary to introduce multiple levels and combinations of the grouping principles under scrutiny. This includes varying the relative strengths of each grouping principle on its own and with respect to other grouping cues. This would allow the construction of *grouping operating characteristics* (GOC) that would show the precise way in which grouping principles trade off against others (Kubovy & van den Berg, 2008).

Finally, in Experiments 2, 5 and 6 (see Chapters 5 and 7) we aimed to investigate the **neurophysiological correlates** (oscillatory brain activity) **of haptic grouping** by **proximity** and **texture-similarity** when both principles act alone or conjoined within the perceptual scene. We focused on Independent

Component Analysis (ICA) of event related spectral perturbations (ERSP), which are thought to measure the average dynamic changes in amplitude of the frequency spectrum (alpha and beta bands in our study) as a function of time during the task period. Overall, we reach three conclusions.

- The IC clustering analysis of Experiments 2, 5 and 6 revealed the activation of a widespread bilateral network of sensorimotor and parietal areas that seems to be involved in all the stages of the haptic perceptual grouping process: (1) Finger movement and proprioception (left sensorimotor cortex); (2) inhibition of involuntary movements (right sensorimotor cortex); (3) cortical integration of micro and macrospatial features (left parietal cortex); and (4) the integration of spatial information and sensorimotor behavior (right parietal cortex). Interestingly, we only found activation of the occipital (visual) cortex in Experiments 5 and 6 but not in Experiment 2. This result could be related to the distinct nature of the tasks performed. In this line, some studies have found the involvement of visual areas in tactile tasks, especially when they require the discrimination of macrospatial features but not when the task is based on the discrimination of low-level microspatial features (Stoesz et al., 2003). Thus, the activity found in the visual cortex in the non-attentional tasks of this study could be related to the fact that discrimination between textures and spatial proximities was not the explicit goal of the task. Thus, the participants may have needed to form a visual representation of the tactile stimulus after the integration of low-level features.
- 2. The different ERD/ERS timing of the ERSP over the active areas during the performance of the grouping task indicates the existence of differences in the

required cognitive demands between grouping conditions. Specifically, the ERD differences found in both sensorimotor cortices (Experiment 2) might reflect the different exploration timing and demands required in the processing of global/holistic (proximity) and local (similarity) features, respectively. In addition, the more pronounced alpha ERD over the contralateral parietal cortex in the similarity condition (Experiment 2) could be explained by the greater feature and spatial integration demands of this grouping condition.

Finally, the results from Experiments 5 and 6 that include conditions in which grouping principles acted conjoined within the same stimulus showed the activation of the right dorsolateral prefrontal cortex. This area has been linked to the manipulation of non-verbal information, especially during the performance of working memory tasks. Interestingly, the strong connections between prefrontal and parietal cortices are thought to form a circuit responsible for the transfer from unimodal integration areas to multimodal areas where information is manipulated and updated online (Petrides & Pandya, 1984). Moreover, this circuit is also involved in tactile object discrimination. According to this, the conjoined activation found on prefrontal and parietal areas in Experiments 5 and 6 could be related to: 1) the integration of the disjointed individual features of each tactile stimulus into an integrated or unified percept; and 2) the maintenance, manipulation and updating of this information during haptic exploration (Stoeckel et al., 2003). Finally, the integrated (grouped) information may be used to decide the appropriate response according to the different stimulus configuration. This explanation also agrees with the more intense ERD found in the

competitive condition in Experiment 5, when proximity was the interfering cue. This result is in accordance with the dominance of proximity grouping over texture similarity. The enhanced activity in this grouping condition may result from the greater cognitive demands when participants try to integrate the proximity incongruent cues into a coherent and stable percept.

As a final remark, we expect that the methods and results presented in this Thesis constitute a first step into the quantitative experimental research of the perceptual organization process in the sense of touch. A powerful and more complete understanding of these processes may have a great potential in terms of practical applications. For example, this greater understanding will be useful in the development of multisensory interfaces, in a world in which smart devices increasingly combine information from multiple sensory modalities, including vision, audition and touch. On the other hand, it also could be an interesting venue for the creation and design of sensory substitution devices for visual and auditory impaired people. Finally, future research in this area will also serve as a medium for increasing the knowledge of the neural basis of perceptual organization, and to understand how our brain reaches a useful and adaptive (from an evolutionary point of view) representation of the outside world, by combining and structuring the huge amount of incoming information coming from our senses.

CHAPTER 10:
AGRUPAMIENTO
PERCEPTIVO EN EL
TACTO: CORRELATOS
CONDUCTUALES Y
NEUROFISIOLÓGICOS

Haptic Perceptual Grouping: Behavioral and Neurophysiological Correlates

AGRUPAMIENTO
PERCEPTIVO HÁPTICO:
CORRELATOS
CONDUCTUALES Y
NEUROFISIOLÓGICOS

AUTOR:

Antonio Prieto Lara

INSTITUCIÓN:

Universidad Nacional de Educación a Distancia Departamento de Psicología Básica II

PROGRAMA DE DOCTORADO EN PSICOLOGÍA DE LA SALUD

Directora: Soledad Ballesteros Jiménez **Codirectora:** Julia Mayas Arellano

La organización perceptiva es el proceso que enfrenta a nuestro sistema perceptivo con la tarea de descifrar la información sensorial proveniente del mundo exterior para alcanzar una representación verídica, congruente y útil de nuestro entorno (Ruth Kimchi et al., 2003; Pomerantz & Kubovy, 1981).

Tradicionalmente, se ha considerado el agrupamiento perceptivo como el proceso más íntimamente ligado a la organización perceptiva. Sin embargo, no son sinónimos. El agrupamiento perceptivo constituye un tipo particular de proceso organizativo que determina los elementos cualitativos de nuestra percepción. Consiste, a grandes rasgos, en el hecho de que los observadores perciben algunos

ítems del campo perceptivo como pertenecientes a un mismo conjunto de elementos con más fuerza que otros (Wagemans et al., 2012).

La organización perceptiva y el agrupamiento han sido investigados exhaustivamente en modalidad visual y, en menor medida, en modalidad auditiva. Sin embargo, muy pocos estudios tratan de manera explícita con las cuestiones organizacionales en el tacto, e incluso las revisiones y monografías dedicadas de manera exclusiva a la percepción en esta modalidad han ignorado la cuestión, algo sorprendente dado que el tacto, junto con la vista y el oído, es considerado uno de los sentidos *espaciales* (Gallace & Spence, 2011).

Una de las cuestiones más relevantes en la investigación sobre agrupamiento perceptivo durante los últimos años, es el estudio cuantitativo del funcionamiento interactivo de varios principios de agrupamiento actuando de manera conjunta en la misma escena perceptiva (Kubovy & van den Berg, 2008; Luna, Villalba-García, Montoro, & Hinojosa, 2016; Quinlan & Wilton, 1998; Schmidt & Schmidt, 2013).

Tradicionalmente, esta línea de investigación ha perseguido dos objetivos diferentes: (1) desarrollar un modelo que dé cuenta de los efectos combinados de los diferentes principios de agrupamiento perceptivo cuando estos actúan de manera conjunta y (2), identificar las reglas que determinan que principios dominan la organización percibida cuando dos o más claves de agrupamiento actúan simultáneamente (Han & Humphreys, 1999; Palmer & Beck, 2007; Schmidt & Schmidt, 2013).

Dada la ausencia de investigación que aborde las dinámicas de dominancia de los principios de agrupamiento en el tacto, las leyes que gobiernan tales interacciones, así como las bases neurológicas que subyacen a estos procesos, la presente Tesis doctoral se propone como principal objetivo investigar de manera

cuantitativa como diferentes principios de agrupamiento perceptivo (proximidad espacial y similaridad en textura), interaccionan durante el proceso de organización perceptiva en el tacto para dar lugar a los objetos que conforman la percepción táctil.

Para lograr este fin se realizaron 6 experimentos divididos en 4 diferentes estudios, en los que se abordaron de manera exhaustiva los objetivos específicos derivados del objetivo principal perfilado en el párrafo anterior: (1) Analizar el curso temporal y las dinámicas de dominancia de los principios de agrupamiento en la modalidad háptica; (2) investigar las interacciones entre principios de agrupamiento en el tacto, así como su compatibilidad con un modelo aditivo de los efectos de agrupamiento y (3), investigar los correlatos neurofisiológicos (actividad cerebral oscilatoria) del agrupamiento perceptivo en el tacto cuando diferentes principios de agrupamiento actúan de manera aislada o conjunta dentro de la misma escena estimular.

En el primero de los estudios (Experimento 1) se investigaron las dinámicas de dominancia de los principios de agrupamiento en la modalidad háptica. Para ello se compararon las respuestas a estímulos agrupados mediante proximidad espacial con aquellas a estímulos agrupados por similaridad en textura, utilizando una tarea de detección de la orientación en la que los estímulos táctiles se combinaron para formar patrones horizontales/verticales, de acuerdo con uno de los citados principios de agrupamiento. Los resultados del estudio indicaron que los participantes fueron más rápidos detectando la orientación de los estímulos agrupados por proximidad espacial, respecto a aquellos agrupados por similaridad en textura. Adicionalmente, la orientación de los estímulos fue detectada más

rápidamente cuando estos estuvieron orientados verticalmente, pero tan solo cuando se encontraban agrupados por proximidad espacial.

El segundo estudio (Experimento 2), se investigaron las dinámicas de dominancia y los correlatos neuronales del agrupamiento mediante proximidad espacial y similaridad en textura en modalidad háptica. Se analizaron las respuestas conductuales y la actividad oscilatoria cerebral en las bandas alfa y beta durante una tarea de detección de la orientación que reproducía la utilizada en el Estudio 1 de la presente Tesis. Los resultados conductuales mostraron una identificación de la orientación más rápida y con menos errores en aquellos estímulos agrupados por proximidad espacial, un resultado que concuerda con lo encontrado en el Estudio 1. Por otro lado, el análisis de componentes independientes (ICA-clustering), reveló la participación de una red bilateral de áreas sensoriomotoras y parietales en la detección de la orientación de estímulos agrupados mediante principios de agrupamiento.

En el estudio número 3 (Experimentos 3 y 4), se investigaron las interacciones entre los principios de agrupamiento de proximidad espacial y similaridad en textura en la modalidad háptica. Para ello, se adaptaron al tacto dos paradigmas ampliamente utilizados en modalidad visual. En el Experimento 3 se empleó una tarea fenomenológica experimental, consistente en clasificar la fuerza subjetiva de agrupamiento, tanto en condiciones en las que cada principio de agrupamiento actuaba por separado, como en condiciones en las que ambos principios actuaban de manera conjunta (cooperativa o competitivamente). En el Experimento 4, por otra parte, los participantes realizaron una tarea psicofísica, en la que una respuesta objetiva (in)correcta se definió previamente mediante la atención

selectiva a una clave de agrupamiento particular en diferentes bloques de ensayos. En ambos experimentos, los resultados mostraron que la proximidad espacial dominó la organización de la escena táctil sobre la similaridad en textura cuando ambos principios competieron dentro de la misma escena perceptiva. Añadido a lo anterior, los resultados obtenidos son compatibles con un modelo aditivo de los efectos del agrupamiento, de manera similar a lo ocurrido en otras modalidades perceptivas.

Finalmente, en el estudio número 4 (Experimentos 5 y 6) se investigaron los correlatos conductuales y neurofisiológicos de las interacciones entre los principios de agrupamiento de proximidad espacial y similaridad en textura en el tacto, mediante dos diferentes adaptaciones de la tarea de discriminación de la repetición (RDT) empleada anteriormente en modalidad visual. Estas tareas proporcionan una medida indirecta que no requiere de atención explícita al proceso de agrupamiento, manteniendo, al mismo tiempo, una respuesta (in)correcta definida objetivamente. En el Experimento 5 se presentó a los participantes una fila de elementos que se alternaban en textura, excepto dos de los elementos en los que la textura se repetía. Los participantes tuvieron que decidir si los estímulos en los que se repetía la textura (agrupamiento por similaridad) eran lisos o rugosos en diferentes condiciones de proximidad espacial entre objetivos y distractores, que podían bien facilitar o dificultar la respuesta a la tarea. En el Experimento 6, los participantes debían indicar que cohorte (definida por la proximidad espacial entre sus elementos) contenía un mayor número de elementos, mientras en diferentes condiciones experimentales se modificaba la similaridad en textura dentro de y entre las diferentes cohortes. Los resultados indican la compatibilidad de los efectos de agrupamiento encontrados con un modelo aditivo (en concordancia con lo obtenido en los Experimentos 3 y 4 del Estudio 3). Por otro lado, el principio de proximidad espacial parece dominar el proceso de agrupamiento perceptivo cuando ambos principios actúan de manera conjunta, dada las respuestas más rápidas y la menor interferencia/facilitación de estas cuando se dieron ante estímulos agrupados por proximidad (Experimento 6). Estos resultados de nuevo concuerdan con los de los anteriores Estudios (1, 2 y 3). Por último, el análisis de componentes independientes (ICA-clustering) realizado sobre los datos electrofisiológicos reveló la implicación de una extensa red de áreas sensoriomotoras, prefrontales, parietales y occipitales en ambos experimentos. Particularmente interesante fue la mayor activación encontrada en áreas prefrontales dorsolaterales y parietales del hemisferio derecho en la condición de competición entre principios de agrupamiento.

Tomados de manera global, los resultados de la presente Tesis indican que: (1) el agrupamiento por proximidad espacial parece dominar los procesos de organización perceptiva en el tacto cuando actúa de manera conjunta con el principio de similaridad en textura (aunque sin eliminar la influencia de este último); (2) los resultados encontrados son compatibles con un modelo aditivo de los efectos combinados de los diferentes principios de agrupamiento perceptivo; y (3) el análisis de los datos neurofisiológicos, revela la implicación de una amplia red de áreas sensoriomotoras, parietales y pre-frontales en las tareas de agrupamiento perceptivo en el tacto. Esta activación difiere entre los diferentes principios de agrupamiento, indicando la existencia de diferencias en las demandas cognitivas asociadas a cada uno de estos principios. Por último, la mayor activación de las áreas prefrontales y parietales encontrada en condiciones de competición entre principios de agrupamiento (Experimentos 5 y 6), parece

estar relacionada con las mayores demandas de mantenimiento, manipulación e integración de la información cuando los participantes deben gestionar la presencia de información contradictoria para formar un percepto (objeto) final.

Los métodos y resultados presentados en esta Tesis pretenden constituir un primer paso en la investigación experimental cuantitativa de los procesos de organización perceptiva en el sentido del tacto. Un conocimiento más profundo y completo de estos procesos podría tener un gran potencial en términos de aplicaciones prácticas, como el desarrollo de interfaces multisensoriales o la creación de sistemas de sustitución sensorial para personas con dificultades visuales y/o auditivas. La investigación en esta área podría servir también como un medio para profundizar en el conocimiento de las bases neuronales de la organización perceptiva, así como para conocer la forma en que nuestro cerebro alcanza una representación útil y adaptativa (desde un punto de vista evolutivo) del mundo exterior, a través de la selección y estructuración de la inmensa cantidad de información proveniente de nuestros sentidos.

Haptic Perceptual Grouping: Behavioral and Neurophysiological Correlates

REFERENCES

Haptic Perceptual Grouping: Behavioral and Neurophysiological Correlates

- Aissani, C., Martinerie, J., Yahia-Cherif, L., Paradis, A. L., & Lorenceau, J. (2014).

 Beta, but not gamma, band oscillations index visual form-motion integration.

 PLoS ONE, 9(4). https://doi.org/10.1371/journal.pone.0095541
- Alais, D., Blake, R., & Lee, S. H. (1998). Visual features that vary together over time group together over space. *Nature Neuroscience*, 1(2), 160–164. https://doi.org/10.1038/414
- Amazeen, E. L., & Turvey, M. T. (1996). Weight Perception and the Haptic Size-Weight Illusion Are Functions of the Inertia Tensor. *Journal of Experimental Psychology: Human Perception and Performance*, 22(1), 213–232. https://doi.org/10.1037/0096-1523.22.1.213
- Amedi, a, Malach, R., Hendler, T., Peled, S., & Zohary, E. (2001). Visuo-haptic object-related activation in the ventral visual pathway. *Nature Neuroscience*, *4*(3), 324–330. https://doi.org/10.1038/85201
- Anscombe, f. J. (1948). The transformation of poisson, binomial and negative-binomial data. *Biometrika*, 35(3–4), 246–254. https://doi.org/10.1093/biomet/35.3-4.246
- Awh, E., Vogel, E. K., & Oh, S. H. (2006). Interactions between attention and working memory. *Neuroscience*, 139(1), 201–208. https://doi.org/10.1016/j.neuroscience.2005.08.023
- Babiloni, C., Carducci, F., Cincotti, F., Rossini, P. M., Neuper, C., Pfurtscheller, G., & Babiloni, F. (1999). Human Movement-Related Potentials vs Desynchronization of EEG Alpha Rhythm: A High-Resolution EEG Study. *NeuroImage*, *10*(6), 658–665. https://doi.org/10.1006/nimg.1999.0504
- Baker, S. N. (2007). Oscillatory interactions between sensorimotor cortex and the periphery. *Current Opinion in Neurobiology*.

- https://doi.org/10.1016/j.conb.2008.01.007
- Ballesteros, S., & Heller, M. A. (2008). Haptic object identification. In *Human Haptic Perception: Basics and Applications* (pp. 207–222). https://doi.org/10.1007/978-3-7643-7612-3_16
- Ballesteros, S., Manga, D., & Reales, J. M. (1997). Haptic discrimination of bilateral symmetry in 2-dimensional and 3-dimensional unfamiliar displays. *Perception and Psychophysics*, *59*(1), 37–50. https://doi.org/10.3758/BF03206846
- Ballesteros, S., Mayas, J., Reales, J. M., & Heller, M. (2012). The Effect of Age on the Haptic Horizontal-Vertical Curvature Illusion With Raised-Line Shapes.

 Developmental Neuropsychology, 37(8), 653–667.

 https://doi.org/10.1080/87565641.2012.688901
- Ballesteros, S., Millar, S., & Reales, J. M. (1998). Symmetry in haptic and in visual shape perception. *Perception and Psychophysics*, 60(3), 389–404. https://doi.org/10.3758/BF03206862
- Ballesteros, S., Muñoz, F., Sebastián, M., García, B., & Reales, J. M. (2009). ERP evidence of tactile texture processing: Effects of roughness and movement. In Proceedings 3rd Joint EuroHaptics Conference and Symposium on Haptic Interfaces for Virtual Environment and Teleoperator Systems, World Haptics 2009 (pp. 166–171). https://doi.org/10.1109/WHC.2009.4810901
- Ballesteros, S., & Reales, J. M. (2004). Visual and haptic discrimination of symmetry in unfamiliar displays extended in the z-axis. *Perception*, *33*(3), 315–327. https://doi.org/10.1068/p5017
- Ballesteros, S., & Reales, J. M. (2005). Haptic priming and recognition in young adults, normal aging, and alzheimer's disease: Evidence for dissociable memory systems. *Touch and Blindness: Psychology and Neuroscience*, 42(8),

- 1063-1070. https://doi.org/10.4324/9781410615671
- Ballesteros, S., Reales, J. M., De Leon, L. P., & Garcia, B. (2005). The perception of ecological textures by touch: Does the perceptual space change under bimodal visual and haptic exploration? In *Proceedings 1st Joint Eurohaptics Conference and Symposium on Haptic Interfaces for Virtual Environment and Teleoperator Systems; World Haptics Conference, WHC 2005* (pp. 635–638). https://doi.org/10.1109/WHC.2005.134
- Baraldi, P., Porro, C. A., Serafini, M., Pagnoni, G., Murari, C., Corazza, R., & Nichelli, P. (1999). Bilateral representation of sequential finger movements in human cortical areas. *Neuroscience Letters*, *269*(2), 95–98. https://doi.org/10.1016/S0304-3940(99)00433-4
- Bell, A. J., & Sejnowski, T. J. (1995). An information-maximization approach to blind separation and blind deconvolution. *Neural Computation*, 7(6), 1129–59. https://doi.org/10.1162/neco.1995.7.6.1129
- Ben-Av, M. B., & Sagi, D. (1995). Perceptual grouping by similarity and proximity: Experimental results can be predicted by intensity autocorrelations. *Vision Research*, *35*(6), 853–866. https://doi.org/10.1016/0042-6989(94)00173-J
- Bensmaïa, S., Hollins, M., & Yau, J. (2005). Vibrotactile intensity and frequency information in the Pacinian system: A psychophysical model. *Perception & Psychophysics*, 67(5), 828–841.
- Binkofski, F., Buccino, G., Stephan, K. M., Rizzolatti, G., Seitz, R. J., & Freund, H. J. (1999). A parieto-premotor network for object manipulation: Evidence from neuroimaging. In *Experimental Brain Research* (Vol. 128, pp. 210–213). https://doi.org/10.1007/s002210050838
- Blankenburg, F., Ruff, C. C., Deichmann, R., Rees, G., & Driver, J. (2006). The

- cutaneous rabbit illusion affects human primary sensory cortex somatotopically. *PLoS Biology*, *4*(3), 0459–0466. https://doi.org/10.1371/journal.pbio.0040069
- Blum, J., Lutz, K., & Jäncke, L. (2007). Coherence and phase locking of intracerebral activation during visuo- and audio-motor learning of continuous tracking movements. *Experimental Brain Research*, 182(1), 59–69. https://doi.org/10.1007/s00221-007-0963-7
- Bodegård, A., Geyer, S., Grefkes, C., Zilles, K., & Roland, P. E. (2001). Hierarchical processing of tactile shape in the human brain. *Neuron*, *31*(2), 317–328. https://doi.org/10.1016/S0896-6273(01)00362-2
- Boecker, H., Khorram-Sefat, D., Kleinschmidt, A., Merboldt, K.-D., Hänicke, W., Requardt, M., & Frahm, J. (1995). High-resolution functional magnetic resonance imaging of cortical activation during tactile exploration. *Human Brain Mapping*, *3*(3), 236–244. https://doi.org/10.1002/hbm.460030307
- Boonstra, T. W., Daffertshofer, A., Breakspear, M., & Beek, P. J. (2007). Multivariate time-frequency analysis of electromagnetic brain activity during bimanual motor learning. *NeuroImage*, *36*(2), 370–377. https://doi.org/10.1016/j.neuroimage.2007.03.012
- Brovelli, A., Ding, M., Ledberg, A., Chen, Y., Nakamura, R., & Bressler, S. L. (2004).

 Beta oscillations in a large-scale sensorimotor cortical network: Directional influences revealed by Granger causality. *Proceedings of the National Academy of Sciences*, 101(26), 9849–9854. https://doi.org/10.1073/pnas.0308538101
- Bryden, M. P. (1977). Measuring handedness with questionnaires. *Neuropsychologia*, 15(4–5), 617–624. https://doi.org/10.1016/0028-3932(77)90067-7

- Burton, H., Fabri, M., & Alloway, K. (1995). Cortical areas within the lateral sulcus connected to cutaneous representations in areas 3b and 1: A revised interpretation of the second somatosensory area in macaque monkeys.

 Journal of Comparative Neurology, 355(4), 539–562.

 https://doi.org/10.1002/cne.903550405
- Cardinali, L., Frassinetti, F., Brozzoli, C., Urquizar, C., Roy, A. C., & Farnè, A. (2009).

 Tool-use induces morphological updating of the body schema (DOI:10.1016/j.cub.2009.05.009).

 Current Biology. https://doi.org/10.1016/j.cub.2009.06.048
- Chan, J. S., & Newell, F. N. (2008). Behavioral evidence for task-dependent "what" versus "where" processing within and across modalities. *Perception and Psychophysics*, 70(1), 36–49. https://doi.org/10.3758/PP.70.1.36
- Chang, D., Nesbitt, K. V., & Wilkins, K. (2007a). The Gestalt principle of continuation applies to both the haptic and visual grouping of elements. In *Proceedings Second Joint EuroHaptics Conference and Symposium on Haptic Interfaces for Virtual Environment and Teleoperator Systems, World Haptics 2007* (pp. 15–20). https://doi.org/10.1109/WHC.2007.113
- Chang, D., Nesbitt, K. V., & Wilkins, K. (2007b). The gestalt principles of similarity and proximity apply to both the haptic and visual grouping of elements. In *Conferences in Research and Practice in Information Technology Series* (Vol. 64, pp. 79–86). https://doi.org/10.1109/WHC.2007.113
- Claessens, P. M., & Wagemans, J. (2005). Perceptual grouping in Gabor lattices:

 Proximity and alignment. *Attention, Perception, & Psychophysics*, *67*(8), 1446–1459.
- Classen, J., Gerloff, C., Honda, M., Hallett, M., Andrew, C., Pfurtscheller, G., ...

- Caminiti, R. (1998). Integrative visuomotor behavior is associated with interregionally coherent oscillations in the human brain. *Journal of Neurophysiology*, 79(3), 1567–73. https://doi.org/10.1007/bf02520079
- Cohen, M. X., & Ridderinkhof, K. R. (2013). EEG Source Reconstruction Reveals Frontal-Parietal Dynamics of Spatial Conflict Processing. *PLoS ONE*, 8(2). https://doi.org/10.1371/journal.pone.0057293
- Collins, C. C. (1970). Tactile Television-Mechanical and Electrical Image Projection. *IEEE Transactions on Man-Machine Systems*, 11(1), 65–71.

 https://doi.org/10.1109/TMMS.1970.299964
- Corbetta, M., & Shulman, G. L. (2002). CONTROL OF GOAL-DIRECTED AND STIMULUS-DRIVEN ATTENTION IN THE BRAIN. *Nature Reviews Neuroscience*, 3(3), 215–229. https://doi.org/10.1038/nrn755
- D'Esposito, M., Aguirre, G. K., Zarahn, E., Ballard, D., Shin, R. K., & Lease, J. (1998). Functional MRI studies of spatial and nonspatial working memory. *Cognitive Brain Research*, 7(1), 1–13. https://doi.org/10.1016/S0926-6410(98)00004-4
- Dakin, S. C. (2015). Seeing Statistical Regularities: Texture and Pattern Perception. *The Oxford Handbook of Perceptual Organization*, 150–167.

 https://doi.org/10.1093/oxfordhb/9780199686858.013.054
- Davis, N. J., Tomlinson, S. P., & Morgan, H. M. (2012). The Role of Beta-Frequency Neural Oscillations in Motor Control. *Journal of Neuroscience*, *32*(2), 403–404. https://doi.org/10.1523/JNEUROSCI.5106-11.2012
- Delorme, A., & Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, 134(1), 9–21. https://doi.org/10.1016/j.jneumeth.2003.10.009

- Desmurget, M., & Sirigu, A. (2009). A parietal-premotor network for movement intention and motor awareness. *Trends in Cognitive Sciences*, *13*(10), 411–419. https://doi.org/10.1016/j.tics.2009.08.001
- Engel, A. K., & Fries, P. (2010). Beta-band oscillations-signalling the status quo? *Current Opinion in Neurobiology*. https://doi.org/10.1016/j.conb.2010.02.015
- Fagot, J., Arnaud, B., Chlambretto, M., & Fayolle, R. (1992). Lateralization in haptic processing: An apparatus for analyzing manual strategies. *Behavior Research Methods, Instruments, & Computers, 24*(1), 54–59. https://doi.org/10.3758/BF03203470
- Fitzgerald, P. J., Lane, J. W., Thakur, P. H., & Hsiao, S. S. (2006). Receptive Field Properties of the Macaque Second Somatosensory Cortex: Representation of Orientation on Different Finger Pads. *Journal of Neuroscience*, 26(24), 6473–6484. https://doi.org/10.1523/JNEUROSCI.5057-05.2006
- Flach, R., & Haggard, P. (2006). The cutaneous rabbit revisited. *Journal of Experimental Psychology: Human Perception and Performance*, 32(3), 717.
- Fleischman, D. A. (2007). Repetition priming in aging and Alzheimer's disease: An integrative review and future directions. *Cortex*. https://doi.org/10.1016/S0010-9452(08)70688-9
- Fletcher, P. C., & Henson, R. N. (2001). Frontal lobes and human memory: insights from functional neuroimaging. *Brain : A Journal of Neurology, 124*(Pt 5), 849–881. https://doi.org/10.1093/brain/124.5.849
- Flevaris, A. V., & Robertson, L. C. (2016). Spatial frequency selection and integration of global and local information in visual processing: A selective review and tribute to Shlomo Bentin. *Neuropsychologia*, *83*, 192–200. https://doi.org/10.1016/j.neuropsychologia.2015.10.024

- Frehlich, M., Dominguez, L. G., Atluri, S., Radhu, N., Sun, Y., Daskalakis, Z. J., & Farzan, F. (2016). Unbiased cluster estimation of electrophysiological brain response. *Journal of Neuroscience Methods*, *271*, 43–49. https://doi.org/10.1016/j.jneumeth.2016.06.020
- Gaetz, W., & Cheyne, D. (2006). Localization of sensorimotor cortical rhythms induced by tactile stimulation using spatially filtered MEG. *NeuroImage*, *30*(3), 899–908. https://doi.org/10.1016/j.neuroimage.2005.10.009
- Gallace, A., & Spence, C. (2008). The cognitive and neural correlates of "tactile consciousness": A multisensory perspective. *Consciousness and Cognition*. https://doi.org/10.1016/j.concog.2007.01.005
- Gallace, A., & Spence, C. (2011). To what extent do Gestalt grouping principles influence tactile perception? *Psychological Bulletin*, *137*(4), 538–561. https://doi.org/10.1037/a0022335
- Gallace, A., Tan, H. Z., & Spence, C. (2007). The body surface as a communication system: The state of the art after 50 years. *Presence: Teleoperators and Virtual Environments*. https://doi.org/10.1162/pres.16.6.655
- Gardony, A. L., Eddy, M. D., Brunyé, T. T., & Taylor, H. A. (2017). Cognitive strategies in the mental rotation task revealed by EEG spectral power. *Brain and Cognition*, *118*, 1–18. https://doi.org/10.1016/j.bandc.2017.07.003
- Gazzaniga, M. S., Ivry, R. B., & Mangun, G. R. (2009). Cognitive Neuroscience: The Biology of the Mind. *The Quarterly Review of Biology*. https://doi.org/10.1086/603482
- Gentaz, E., Baud-Bovy, G., & Luyat, M. (2008). The haptic perception of spatial orientations. *Experimental Brain Research*, *187*(3), 331.
- Gibson, J. J. (1979). The Ecological Approach to Visual Perception. Gibson, J.J. (1979).

- The Ecological Approach to Visual Perception. Boston: Houghton Mifflin.ISBN 0898599598 (1986) (Vol. 39).
- Gomez-Ramirez, M., Hysaj, K., & Niebur, E. (2016). Neural mechanisms of selective attention in the somatosensory system. *Journal of Neurophysiology*, *116*(3), 1218–1231. https://doi.org/10.1152/jn.00637.2015
- Goodwin, a W., Macefield, V. G., & Bisley, J. W. (1997). Encoding of object curvature by tactile afferents from human fingers. *Journal of Neurophysiology*, *78*(6), 2881–2888. https://doi.org/10.1152/jn.1997.78.6.2881
- Goodwin, A. W., & Wheat, H. E. (2008). Physiological mechanisms of the receptor system. In *Human Haptic Perception: Basics and Applications* (pp. 93–102). https://doi.org/10.1007/978-3-7643-7612-3_7
- Grandchamp, R., & Delorme, A. (2011). Single-trial normalization for event-related spectral decomposition reduces sensitivity to noisy trials. *Frontiers in Psychology*, *2*(SEP). https://doi.org/10.3389/fpsyg.2011.00236
- Greenspan, J. D., & Winfield, J. A. (1992). Reversible pain and tactile deficits associated with a cerebral tumor compressing the posterior insula and parietal operculum. *Pain*, *50*(1), 29–39. https://doi.org/10.1016/0304-3959(92)90109-0
- Grill-Spector, K., Kourtzi, Z., & Kanwisher, N. (2001). The lateral occipital complex and its role in object recognition. In *Vision Research* (Vol. 41, pp. 1409–1422). https://doi.org/10.1016/S0042-6989(01)00073-6
- Gross, J., Pollok, B., Dirks, M., Timmermann, L., Butz, M., & Schnitzler, A. (2005).

 Task-dependent oscillations during unimanual and bimanual movements in the human primary motor cortex and SMA studied with magnetoencephalography.

 NeuroImage, 26(1), 91–98.

- https://doi.org/10.1016/j.neuroimage.2005.01.025
- Grunwald, M. (2008). *Human haptic perception: Basics and applications. Human Haptic Perception: Basics and Applications*. https://doi.org/10.1007/978-3-7643-7612-3
- Haaland, K. Y., Elsinger, C. L., Mayer, A. R., Durgerian, S., & Rao, S. M. (2004). Motor Sequence Complexity and Performing Hand Produce Differential Patterns of Hemispheric Lateralization. *Journal of Cognitive Neuroscience*, *16*(4), 621–636. https://doi.org/10.1162/089892904323057344
- Halata, Z., & Baumann, K. I. (2008). Anatomy of receptors. In *Human Haptic Perception: Basics and Applications* (pp. 85–92). https://doi.org/10.1007/978-3-7643-7612-3_6
- Han, S. (2004). Interactions between proximity and similarity grouping: An event-related brain potential study in humans. *Neuroscience Letters*, *367*(1), 40–43. https://doi.org/10.1016/j.neulet.2004.05.098
- Han, S., Ding, Y., & Song, Y. (2002). Neural mechanisms of perceptual grouping in humans as revealed by high density event related potentials. *Neuroscience Letters*, *319*(1), 29–32. https://doi.org/10.1016/S0304-3940(01)02502-2
- Han, S., & Humphreys, G. W. (1999). Interactions between perceptual organization based on Gestalt laws and those based on hierarchical processing. *Perception and Psychophysics*, *61*(7), 1287–1298. https://doi.org/10.3758/BF03206180
- Han, S., Song, Y., Ding, Y., Yund, E. W., & Woods, D. L. (2001). Neural substrates for visual perceptual grouping in humans. *Psychophysiology*, 38, 926–935. https://doi.org/10.1111/1469-8986.3860926
- Heitger, F., von der Heydt, R., Peterhans, E., Rosenthaler, L., & Kübler, O. (1998). Simulation of neural contour mechanisms: representing anomalous contours.

- *Image and Vision Computing.* https://doi.org/10.1016/S0262-8856(97)00083-8
- Heller, M. A. (2013). The psychology of touch. Psychology Press.
- Heller, M. A., & Ballesteros, S. (2005). *Touch and Blindness: Psychology and Neuroscience*. *Touch and Blindness: Psychology and Neuroscience*. https://doi.org/10.4324/9781410615671
- Heller, M. A., & Joyner, T. D. (1993). Mechanisms in the haptic horizontal-vertical illusion: Evidence from sighted and blind subjects. *Perception & Psychophysics*, 53(4), 422–428. https://doi.org/10.3758/BF03206785
- Heller, M. A., Wilson, K., Steffen, H., Yoneyama, K., & Brackett, D. D. (2003). Superior haptic perceptual selectivity in late-blind and very-low-vision subjects. *Perception*, *32*(4), 499–511. https://doi.org/10.1068/p3423
- Ho, H., & Jones, L. A. (2004). Material identification using real and simulated thermal cues. In *Engineering in Medicine and Biology Society, 2004. IEMBS'04.*26th Annual International Conference of the IEEE (Vol. 1, pp. 2462–2465).

 IEEE.
- Hochberg, J., & Hardy, D. (1960). Brightness and proximity factors in grouping.

 *Perceptual & Motor Skills, 10, 22.
- Hochberg, J., & Silverstein, A. (1956). A quantitative index of stimulus-similarity proximity vs. differences in brightness. *The American Journal of Psychology*, 69(3), 456–458. https://doi.org/10.2307/1419052
- Hsiao, S. S., Lane, J., & Fitzgerald, P. (2002). Representation of orientation in the somatosensory system. *Behavioural Brain Research*, *135*(1–2), 93–103.
- Hsiao, S., & Yau, J. (2008). Neural basis of haptic perception BT Human Haptic Perception: Basics and Applications. In M. Grunwald (Ed.) (pp. 103–112).

- Basel: Birkhäuser Basel. https://doi.org/10.1007/978-3-7643-7612-3_8
- Hubel, D. H., & Wiesel, T. N. (1959). Receptive fields of single neurones in the cat's striate cortex. *The Journal of Physiology*, 148(3), 574–591. https://doi.org/10.1113/jphysiol.1959.sp006308
- Hummel, F., Kirsammer, R., & Gerloff, C. (2003). Ipsilateral cortical activation during finger sequences of increasing complexity: Representation of movement difficulty or memory load? *Clinical Neurophysiology*, *114*(4), 605–613. https://doi.org/10.1016/S1388-2457(02)00417-0
- Ide, C., Kumagai, K., & Hayashi, S. (1985). Freeze-fracture study of the mechanoreceptive digital corpuscles of mice. *Journal of Neurocytology*, 14(6), 1037–1052. https://doi.org/10.1007/BF01224811
- James, T. W., Humphrey, G. K., Gati, J. S., Servos, P., Menon, R. S., & Goodale, M. A. (2002). Haptic study of three-dimensional objects activates extrastriate visual areas. *Neuropsychologia*, *40*(10), 1706–1714. https://doi.org/10.1016/S0028-3932(02)00017-9
- Jiang, W., Tremblay, F., & Chapman, C. E. (1997). Neuronal encoding of texture changes in the primary and the secondary somatosensory cortical areas of monkeys during passive texture discrimination. *Journal of Neurophysiology*, 77(3), 1656–62. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/9084631
- Johansson, R. S. par, Landstrom, U. par, & Lundstrom, R. par. (1982). Responses of mechanoreceptive afferent units in the glabrous skin of the human\par hand to sinusoidal skin displacements.\par. *Brain Res\par*, 244\par(1\par), 17–25\par. https://doi.org/0006-8993(82)90899-X [pii]\par
- Johnson, K. O., Hsiao, S. S., & Yoshioka, T. (2002). Neural coding and the basic law of

- Jung, T.-P., Makeig, S., McKeown, M. J., Bell, A. J., Lee, T.-W., & Sejnowski, T. J. (2001).
 Imaging Brain Dynamics Using Independent Component Analysis. *Proceedings of the IEEE. Institute of Electrical and Electronics Engineers*, 89(7), 1107–1122.
 https://doi.org/10.1109/5.939827
- Kaas, A. L., van Mier, H., Visser, M., & Goebel, R. (2013). The neural substrate for working memory of tactile surface texture. *Human Brain Mapping*, 34(5), 1148–1162. https://doi.org/10.1002/hbm.21500
- Kanizsa, G. (1976). Subjective contours. *Scientific American*, *234*(4), 48–52. https://doi.org/10.1038/scientificamerican0476-48
- Kappers, A. M. L. (2007). Haptic space processing--Allocentric and egocentric reference frames. *Canadian Journal of Experimental Psychology/Revue Canadienne de Psychologie Expérimentale*, 61(3), 208–218. https://doi.org/10.1037/cjep2007022
- Karhu, J., & Tesche, C. D. (1999). Simultaneous early processing of sensory input in human primary (SI) and secondary (SII) somatosensory cortices. *J Neurophysiol*, 81(5), 2017–2025. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/10322043%5Cnhttp://www.mendele y.com/research/simultaneous-early-processing-sensory-input-human-primary-si-secondary-sii-somatosensory-cortices/
- Kelley, W. M., Miezin, F. M., McDermott, K. B., Buckner, R. L., Raichle, M. E., Cohen, N. J., ... Petersen, S. E. (1998). Hemispheric specialization in human dorsal frontal cortex and medial temporal lobe for verbal and nonverbal memory encoding.
 Neuron, 20(5), 927–936. https://doi.org/10.1016/S0896-6273(00)80474-2

- Kienker, P. K., Sejnowski, T. J., Hinton, G. E., & Schumacher, L. E. (1986). Separating figure from ground with a parallel network. *Perception*, *15*(2), 197–216. https://doi.org/10.1068/p150197
- Kimchi, R. (1994). The role of wholistic/configural properties versus global properties in visual form perception. *Perception*, *23*(5), 489–504. https://doi.org/10.1068/p230489
- Kimchi, R. (2000). The perceptual organization of visual objects: A microgenetic analysis. In *Vision Research* (Vol. 40, pp. 1333–1347). https://doi.org/10.1016/S0042-6989(00)00027-4
- Kimchi, R., Behrmann, M., & Olson, C. R. (2003). Perceptual organization in vision:

 Behavioral and neural perspectives. Perceptual Organization in Vision:

 Behavioral and Neural Perspectives. https://doi.org/10.4324/9781410608918
- Kimchi, R., & Bloch, B. (1998). Dominance of configural properties in visual form perception. *Psychonomic Bulletin & Review*, *5*(1), 135–139. https://doi.org/10.3758/BF03209469
- Kimchi, R., & Razpurker-Apfeld, I. (2004). Perceptual grouping and attention: not all groupings are equal. *Psychonomic Bulletin & Review*, 11(4), 687–696. https://doi.org/10.3758/BF03196621
- Kitada, R., Hashimoto, T., Kochiyama, T., Kito, T., Okada, T., Matsumura, M., ... Sadato, N. (2005). Tactile estimation of the roughness of gratings yields a graded response in the human brain: An fMRI study. *NeuroImage*, *25*(1), 90–100. https://doi.org/10.1016/j.neuroimage.2004.11.026
- Kitagawa, N., Igarashi, Y., & Kashino, M. (2009). The Tactile Continuity Illusion. *Journal of Experimental Psychology: Human Perception and Performance*, *35*(6),

 1784–1790. https://doi.org/10.1037/a0016891

- Kitterle, F. L., Christman, S., & Hellige, J. B. (1990). Hemispheric differences are found in the identification, but not the detection, of low versus high spatial frequencies. *Perception & Psychophysics*, 48(4), 297–306. https://doi.org/10.3758/BF03206680
- Klatzky, R. L., Lederman, S. J., & Reed, C. (1987). There's more to touch than meets the eye: The salience of object attributes for haptics with and without vision.

 *Journal of Experimental Psychology: General, 116(4), 356–369.

 https://doi.org/10.1037/0096-3445.116.4.356
- Klimesch, W., Sauseng, P., & Hanslmayr, S. (2007). EEG alpha oscillations: The inhibition-timing hypothesis. *Brain Research Reviews*. https://doi.org/10.1016/j.brainresrev.2006.06.003
- Klostermann, F., Nikulin, V. V., Kühn, A. A., Marzinzik, F., Wahl, M., Pogosyan, A., ... Curio, G. (2007). Task-related differential dynamics of EEG alpha- and betaband synchronization in cortico-basal motor structures. *European Journal of Neuroscience*, *25*(5), 1604–1615. https://doi.org/10.1111/j.1460-9568.2007.05417.x
- Koffka, K. (2013). *Principles of Gestalt psychology* (Vol. 44). Routledge.
- Köhler, W., & Wallach, H. (1944). Figural After-Effects. An Investigation of Visual Processes. *Proceedings of the American Philosophical Society*, 88(4), 269–357. Retrieved from http://www.jstor.org/stable/985451
- Kubovy, M., & Gepshtein, S. (2003). Perceptual grouping in space and in spacetime: An exercise in phenomenological psychophysics. In *Perceptual Organization in Vision: Behavioral and Neural Perspectives* (pp. 45–85). https://doi.org/10.4324/9781410608918
- Kubovy, M., Holcombe, A. O., & Wagemans, J. (1998). On the Lawfulness of

- Grouping by Proximity. *COGNITIVE PSYCHOLOGY*, *35*, 71–98. https://doi.org/10.1006/cogp.1997.0673
- Kubovy, M., & van den Berg, M. (2008). The Whole Is Equal to the Sum of Its Parts:

 A Probabilistic Model of Grouping by Proximity and Similarity in Regular

 Patterns. *Psychological Review*, 115(1), 131–154.

 https://doi.org/10.1037/0033-295X.115.1.131
- Kubovy, M., & Wagemans, J. (1995). Grouping by proximity and multistability in dot lattices: A Quantitative Gestalt Theory. *Psychological Science*, 6(4), 225– 234. https://doi.org/10.1111/j.1467-9280.1995.tb00597.x
- Lamme, V. A. F. (1995). The Neurophysiology of Figure-Ground Segregation in Primary Visual Cortex. *The Journal of Neuroscience*, *15*(February), 1605–1615.
- Lashley, K. S., Chow, K. L., & Semmes, J. (1951). An examination of the electrical field theory of cerebral integration. *Psychological Review*, *58*(2), 123–136. https://doi.org/10.1037/h0056603
- Lechelt, E. C., Eliuk, J., & Tanne, G. (1976). Perceptual orientational asymmetries: A comparison of visual and haptic space. *Perception & Psychophysics*, *20*(6), 463–469. https://doi.org/10.3758/BF03208283
- Lederman, S. J., & Klatzky, R. L. (2009). Haptic perception: A tutorial. *Attention, Perception & Psychophysics, 71*(7), 1439–1459. https://doi.org/10.3758/APP.71.7.1439
- Lee, T.-W., Girolami, M., & Sejnowski, T. J. (1999). Independent Component Analysis Using an Extended Infomax Algorithm for Mixed Subgaussian and Supergaussian Sources. *Neural Computation*, 11(2), 417–441. https://doi.org/10.1162/089976699300016719
- Li Hegner, Y., Lutzenberger, W., Leiberg, S., & Braun, C. (2007). The involvement of

- ipsilateral temporoparietal cortex in tactile pattern working memory as reflected in beta event-related desynchronization. *NeuroImage*, *37*(4), 1362–1370. https://doi.org/10.1016/j.neuroimage.2007.07.003
- Lin, C. L., Shaw, F. Z., Young, K. Y., Lin, C. T., & Jung, T. P. (2012). EEG correlates of haptic feedback in a visuomotor tracking task. *NeuroImage*, 60(4), 2258–2273. https://doi.org/10.1016/j.neuroimage.2012.02.008
- Lopez-Calderon, J., & Luck, S. J. (2014). ERPLAB: an open-source toolbox for the analysis of event-related potentials. *Frontiers in Human Neuroscience*, 8. https://doi.org/10.3389/fnhum.2014.00213
- Luna, D., & Montoro, P. R. (2011). Interactions between intrinsic principles of similarity and proximity and extrinsic principle of common region in visual perception. *Perception*, *40*(12), 1467–1477. https://doi.org/10.1068/p7086
- Luna, D., Villalba-García, C., Montoro, P. R., & Hinojosa, J. A. (2016). Dominance dynamics of competition between intrinsic and extrinsic grouping cues. *Acta Psychologica*, *170*, 146–154. https://doi.org/10.1016/j.actpsy.2016.07.001
- MacLeod, C. M. (1991). Half a century of research on the Stroop effect: an integrative review. *Psychological Bulletin*, 109(2), 163.
- Makeig, S. (1993). Auditory event-related dynamics of the EEG spectrum and effects of exposure to tones. *Electroencephalography and Clinical Neurophysiology*, 86(4), 283–293. https://doi.org/10.1016/0013-4694(93)90110-H
- Makeig, S., J. Bell., A., Jung, T.-P., & Sejnowski, T. J. (1996). Independent Component

 Analysis of Electroencephalographic Data. *Advances in Neural Information Processing Systems*,

 8,

 145–151.

 https://doi.org/10.1109/ICOSP.2002.1180091

- Makeig, S., Jung, T. P., Bell, A. J., Ghahremani, D., & Sejnowski, T. J. (1997). Blind separation of auditory event-related brain responses into independent components. *Proceedings of the National Academy of Sciences of the United States*of America, 94(20), 10979–84. https://doi.org/10.1073/pnas.94.20.10979
- Mao, L. H., Han, S. H., Guo, C. Y., & Jiang, Y. (2004). Neural mechanisms of perceptual grouping in human visual cortex. *Chinese Science Bulletin*, 49(8), 819–823. https://doi.org/Doi 10.1360/04wc0004
- Marr, D. (1982). Vision: A Computational Investigation into the Human Representation and Processing of Visual Information. Book. Retrieved from papers://e74d72ed-e60d-4d01-b249-70f43c2b74c1/Paper/p803
- Martinovic, J., Lawson, R., & Craddock, M. (2012). Time Course of Information

 Processing in Visual and Haptic Object Classification. *Frontiers in Human*Neuroscience, 6. https://doi.org/10.3389/fnhum.2012.00049
- McFarland, D. J., Miner, L. a, Vaughan, T. M., & Wolpaw, J. R. (2000). Mu and beta rhythm topographies during motor imagery and actual movements. *Brain Topography*, 12(3), 177–186. https://doi.org/10.1007/s00221-009-2062-4
- Melnik, A., Hairston, W. D., Ferris, D. P., & König, P. (2017). EEG correlates of sensorimotor processing: Independent components involved in sensory and motor processing. *Scientific Reports*, 7(1). https://doi.org/10.1038/s41598-017-04757-8
- Merabet, L. B., Swisher, J. D., McMains, S. A., Halko, M. A., Amedi, A., Pascual-Leone, A., & Somers, D. C. (2006). Combined Activation and Deactivation of Visual Cortex During Tactile Sensory Processing. *Journal of Neurophysiology*, 97(2), 1633–1641. https://doi.org/10.1152/jn.00806.2006

- Mognon, A., Jovicich, J., Bruzzone, L., & Buiatti, M. (2011). ADJUST: An automatic EEG artifact detector based on the joint use of spatial and temporal features. *Psychophysiology*, 48(2), 229–240. https://doi.org/10.1111/j.1469-8986.2010.01061.x
- Mullen, T., Delorme, a, Kothe, C., & Makeig, S. (2010). An Electrophysiological Information Flow Toolbox for EEGLAB. *Biol Cybern*, *1*, 2. Retrieved from http://tdlc.ucsd.edu/research/posters/AHM_2011/Mullen_Tim.pdf%5Cnpapers2://publication/uuid/C6B7417D-302F-42DE-9B5A-49B094B3744C
- Navon, D. (1977). Forest before trees: The precedence of global features in visual perception. *Cognitive Psychology*, 9(3), 353–383. https://doi.org/10.1016/0010-0285(77)90012-3
- Navon, D. (1981). Do attention and decision follow perception? Comment on Miller. *Journal of Experimental Psychology: Human Perception and Performance, 7*(6),

 1175–1182. https://doi.org/10.1037/0096-1523.7.6.1175
- Neisser, U. (1967). *Cognitive Psychology. Thinkingjudgement and decision makin*. https://doi.org/10.1126/science.198.4319.816
- Nikolaev, A. R., Gepshtein, S., Kubovy, M., & Van Leeuwen, C. (2008). Dissociation of early evoked cortical activity in perceptual grouping. *Experimental Brain Research*, 186(1), 107–122. https://doi.org/10.1007/s00221-007-1214-7
- Nir, G., & Ben Shahar, O. (2015). How Do Multiple Inducers Group in Perceptual Completion Stimuli Psychophysics and Modeling. *Journal of Vision*, *15*(12), 843. Retrieved from http://dx.doi.org/10.1167/15.12.843
- Ogawa, H. (1996). The Merkel cell as a possible mechanoreceptor cell. *Progress in Neurobiology*. https://doi.org/10.1016/S0301-0082(96)00018-4
- Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh

- inventory. *Neuropsychologia*, 9(1), 97–113. https://doi.org/10.1016/0028-3932(71)90067-4
- Onton, J., Delorme, A., & Makeig, S. (2005). Frontal midline EEG dynamics during working memory. *NeuroImage*, *27*(2), 341–356. https://doi.org/10.1016/j.neuroimage.2005.04.014
- Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J. M. (2011). FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Computational Intelligence and Neuroscience*, 2011. https://doi.org/10.1155/2011/156869
- Oostenveld, R., & Oostendorp, T. F. (2002). Validating the boundary element method for forward and inverse EEG computations in the presence of a hole in the skull. *Human Brain Mapping*, *17*(3), 179–192. https://doi.org/10.1002/hbm.10061
- Overvliet, K. E., Krampe, R. T., & Wagemans, J. (2012). Perceptual grouping in haptic search: The influence of proximity, similarity, and good continuation. *Journal of Experimental Psychology: Human Perception and Performance*, 38(4), 817–821. https://doi.org/10.1037/a0029222
- Overvliet, K. E., Krampe, R. T., & Wagemans, J. (2013). Grouping by Proximity in Haptic Contour Detection. *PLoS ONE*, 8(6). https://doi.org/10.1371/journal.pone.0065412
- Overvliet, K. E., & Plaisier, M. A. (2016). Perceptual Grouping Affects Haptic Enumeration Over the Fingers. *Perception*, 45(1–2), 71–82. https://doi.org/10.1177/0301006615594958
- Overvliet, K. E., & Sayim, B. (2016). Perceptual grouping determines haptic contextual modulation. *Vision Research*, 126, 52–58.

- https://doi.org/10.1016/j.visres.2015.04.016
- Overvliet, K. E., Smeets, J. B. J., & Brenner, E. (2008). The use of proprioception and tactile information in haptic search. *Acta Psychologica*, *129*(1), 83–90. https://doi.org/10.1016/j.actpsy.2008.04.011
- Oyama, T. (1961). Perceptual Grouping as a Function of Proximity. *Perceptual and Motor Skills*, *13*(3), 305–306. https://doi.org/10.2466/pms.1961.13.3.305
- Palmer, S. E. (1992). Common region: A new principle of perceptual grouping.

 *Cognitive Psychology, 24(3), 436–447. https://doi.org/10.1016/0010-0285(92)90014-S
- Palmer, S. E. (1999). Vision science. System, 810.
- Palmer, S. E. (2003). Perceptual organization and grouping. In *Perceptual Organization in Vision: Behavioral and Neural Perspectives* (pp. 3–43). https://doi.org/10.4324/9781410608918
- Palmer, S. E., & Beck, D. M. (2007). The repetition discrimination task: An objective method for studying perceptual grouping. *Perception & Psychophysics*, 69(1), 68–78. https://doi.org/10.3758/BF03194454
- Palmer, S. E., & Hemenway, K. (1978). Orientation and symmetry: Effects of multiple, rotational, and near symmetries. *Journal of Experimental Psychology:*Human Perception and Performance, 4(4), 691–702.

 https://doi.org/10.1037/0096-1523.4.4.691
- Palmer, S. E., & Nelson, R. (2000). Late influences on perceptual grouping: illusory figures. *Perception & Psychophysics*, 62(7), 1321–31. https://doi.org/10.3758/BF03210743
- Palmer, S., & Rock, I. (1994). Rethinking perceptual organization: The role of uniform connectedness. *Psychonomic Bulletin & Review*, 1(1), 29–55.

- https://doi.org/10.3758/BF03200760
- Peterson, M. A. (1994). The proper placement of uniform connectedness. *Psychonomic Bulletin & Review*. https://doi.org/10.3758/BF03210956
- Petrides, M., & Pandya, D. N. (1984). Projections to the frontal cortex from the posterior parietal region in the rhesus monkey. *Journal of Comparative Neurology*, 228(1), 105–116. https://doi.org/10.1002/cne.902280110
- Pfurtscheller, G. (2001). Functional brain imaging based on ERD/ERS. In *Vision Research* (Vol. 41, pp. 1257–1260). https://doi.org/10.1016/S0042-6989(00)00235-2
- Pfurtscheller, G., & Klimesch, W. (1990). Topographical display and interpretation of event-related desynchronization during a visual-verbal task. *Brain Topography*, *3*(1), 85–93. https://doi.org/10.1007/BF01128865
- Pfurtscheller, G., & Neuper, C. (1997). Motor imagery activates primary sensorimotor area in humans. *Neuroscience Letters*, *239*(2–3), 65–68. https://doi.org/10.1016/S0304-3940(97)00889-6
- Pineda, J. A. (2005). The functional significance of mu rhythms: Translating "seeing" and "hearing" into "doing." *Brain Research Reviews*. https://doi.org/10.1016/j.brainresrev.2005.04.005
- Pomerantz, J. R. (1983). Global and local precedence: Selective attention in form and motion perception. *Journal of Experimental Psychology: General*, *112*(4), 516–540. https://doi.org/10.1037/0096-3445.112.4.516
- Pomerantz, J. R., & Kubovy, M. (1981). Perceptual organization: An overview. In *Perceptual Organization* (pp. 423–456).
- Pomerantz, J. R., & Pristach, E. a. (1989). Emergent features, attention, and perceptual glue in visual form perception. *Journal of Experimental Psychology*.

- Human Perception and Performance, 15(4), 635–649. https://doi.org/10.1037/0096-1523.15.4.635
- Postle, B. R., Stern, C. E., Rosen, B. R., & Corkin, S. (2000). An fMRI investigation of cortical contributions to spatial and nonspatial visual working memory.

 NeuroImage, 11(5 I), 409–423. https://doi.org/10.1006/nimg.2000.0570
- Prather, S. C., Votaw, J. R., & Sathian, K. (2004). Task-specific recruitment of dorsal and ventral visual areas during tactile perception. *Neuropsychologia*, *42*(8), 1079–1087. https://doi.org/10.1016/j.neuropsychologia.2003.12.013
- Prieto, A., Mayas, J., & Ballesteros, S. (2014). Time course of grouping by proximity and similarity in a haptic speeded orientation task. Lecture Notes in Computer Science (including subseries Lecture Notes in Artificial Intelligence and Lecture Notes in Bioinformatics) (Vol. 8618). https://doi.org/10.1007/978-3-662-44193-0_47
- Prieto, A., Mayas, J., & Ballesteros, S. (2018). Interaction dynamics between grouping principles in touch: phenomenological and psychophysical evidence. *Psychological Research*, pp. 1–14. https://doi.org/10.1007/s00426-018-1029-0
- Quinlan, P. T., & Wilton, R. N. (1998). Grouping by proximity or similarity?

 Competition between the Gestalt principles in vision. *Perception*, *27*(4), 417–430. https://doi.org/10.1068/p270417
- Razpurker-Apfeld, I., & Kimchi, R. (2007). The time course of perceptual grouping: the role of segregation and shape formation. *Perception & Psychophysics*, 69(5), 732–743. https://doi.org/10.3758/BF03193775
- Reed, C. L., Caselli, R. J., & Farah, M. J. (1996). Tactile agnosia. Underlying impairment and implications for normal tactile object recognition. *Brain*,

- 119(3), 875–888. https://doi.org/10.1093/brain/119.3.875
- Reed, C. L., Klatzky, R. L., & Halgren, E. (2005). What vs. where in touch: An fMRI study.

 NeuroImage, 25(3), 718–726.

 https://doi.org/10.1016/j.neuroimage.2004.11.044
- Révész, G. (1953). Grundprinzipien des menschlichen und tierischen Daseins.

 *Psychologische** Forschung, 24(3), 215–229.

 https://doi.org/10.1007/BF00424461
- Rock, I., Nijhawan, R., Palmer, S., & Tudor, L. (1992). Grouping based on phenomenal similarity of achromatic color. *Perception*, *21*(6), 779–789.
- Roland, P. E., O'Sullivan, B., & Kawashima, R. (1998). Shape and roughness activate different somatosensory areas in the human brain. *Proceedings of the National Academy of Sciences of the United States of America*, 95(6), 3295–3300. https://doi.org/10.1073/pnas.95.6.3295
- Romei, V., Driver, J., Schyns, P. G., & Thut, G. (2011). Rhythmic TMS over parietal cortex links distinct brain frequencies to global versus local visual processing. *Current Biology*, *21*(4), 334–337. https://doi.org/10.1016/j.cub.2011.01.035
- Rowe, J. B., Toni, I., Josephs, O., Frackowiak, R. S., & Passingham, R. E. (2000). The prefrontal cortex: response selection or maintenance within working memory? *Science*, *288*(5471), 1656–1660. https://doi.org/10.1126/science.288.5471.1656
- Rush, G. P. (1937). Visual grouping in relation to age. *Archives of Psychology* (Columbia University), 217, 94.
- Sadato, N., Yonekura, Y., Waki, A., Yamada, H., & Ishii, Y. (1997). Role of the supplementary motor area and the right premotor cortex in the coordination of bimanual finger movements. *J Neurosci*, 17(24), 9667–9674.

- https://doi.org/10.1016/S0168-0102(97)90507-1
- Sathian, K. (2005). Visual cortical activity during tactile perception in the sighted and the visually deprived. *Developmental Psychobiology*. https://doi.org/10.1002/dev.20056
- Sathian, K. (2016). Analysis of haptic information in the cerebral cortex. *Journal of Neurophysiology*, 116(4), 1795–1806. https://doi.org/10.1152/jn.00546.2015
- Schmidt, F., & Schmidt, T. (2013). Grouping principles in direct competition. *Vision Research*, *88*, 9–21. https://doi.org/10.1016/j.visres.2013.06.002
- Scholtz, D. (1957). Die grundsätze der gestaltwahrnehmung in der haptik. *Acta Psychologica*, *13*, 299–333. https://doi.org/10.1016/0001-6918(57)90029-X
- Schumann, F. (1904). Beiträge zur analyse der gesichtswahrnehmungen. JA Barth.
- Sebastián, M., & Ballesteros, S. (2012). Effects of normal aging on event-related potentials and oscillatory brain activity during a haptic repetition priming task. *NeuroImage*, 60(1), 7–20. https://doi.org/10.1016/j.neuroimage.2011.11.060
- Sebastián, M., Reales, J. M., & Ballesteros, S. (2011). Ageing affects event-related potentials and brain oscillations: A behavioral and electrophysiological study using a haptic recognition memory task. *Neuropsychologia*, 49(14), 3967–3980. https://doi.org/10.1016/j.neuropsychologia.2011.10.013
- Sekuler, A. B., & Bennett, P. J. (2001). Generalized Common Fate: Grouping by Common Luminance Changes. *Psychological Science*, *12*(6), 437–444. https://doi.org/10.1111/1467-9280.00382
- Serrien, D. J., Ivry, R. B., & Swinnen, S. P. (2006). Dynamics of hemispheric specialization and integration in the context of motor control. *Nature Reviews Neuroscience*, 7(2), 160–166. https://doi.org/10.1038/nrn1849

- Smith, E. E., & Jonides, J. (1997). Working memory: A view from neuroimaging.

 Cognitive Psychology, 33(1), 5–42. https://doi.org/10.1006/cogp.1997.0658
- Snow, J. C., Strother, L., & Humphreys, G. W. (2014). Haptic Shape Processing in Visual Cortex. *Journal of Cognitive Neuroscience*, 26(5), 1154–1167. https://doi.org/10.1162/jocn_a_00548
- Sochůrková, D., Rektor, I., Jurák, P., & Stančák, A. (2006). Intracerebral recording of self-paced voluntary cortical activity related to movements: Bereitschaftspotential and event-related desynchronization/synchronization. **SEEG Experimental** study. Brain Research, 173(4), 637-649. https://doi.org/10.1007/s00221-006-0407-9
- Spelke, E. S. (1990). Principles of object perception. *Cognitive Science*, *14*(1), 29–56. https://doi.org/10.1016/0364-0213(90)90025-R
- Spence, C. (2012). Cross-modal perceptual organization. *Oxford University Press*, (2007), 1–16. https://doi.org/10.1093/oxfordhb/9780199686858.013.015
- Stephan, K. M., Binkofski, F., Halsband, U., Dohle, C., Wunderlich, G., Schnitzler, A., ... Freund, H. J. (1999). The role of ventral medial wall motor areas in bimanual co-ordination. A combined lesion and activation study. *Brain*, *122*(2), 351–368. https://doi.org/10.1093/brain/122.2.351
- Stilla, R., & Sathian, K. (2008). Selective visuo-haptic processing of shape and texture. *Human Brain Mapping*, 29(10), 1123–1138. https://doi.org/10.1002/hbm.20456
- Stoeckel, M. C., Weder, B., Binkofski, F., Buccino, G., Shah, N. J., & Seitz, R. J. (2003). A fronto-parietal circuit for tactile object discrimination: An event-related fMRI study. *NeuroImage*, 19(3), 1103–1114. https://doi.org/10.1016/S1053-8119(03)00182-4

- Stoesz, M. R., Zhang, M., Weisser, V. D., Prather, S. C., Mao, H., & Sathian, K. (2003).

 Neural networks active during tactile form perception: Common and differential activity during macrospatial and microspatial tasks. In
 International Journal of Psychophysiology (Vol. 50, pp. 41–49).
 https://doi.org/10.1016/S0167-8760(03)00123-5
- Strother, L., Zhou, Z., Vilis, T., & Snow, J. (2016). Lateral occipito-temporal cortex involvement in haptic object recognition: evidence against mere visual imagery . *Journal of Vision* . https://doi.org/10.1167/16.12.514
- Talairach, J., & Tournoux, P. (1988). Co-Planar Stereotaxis Atlas of the Human Brain:

 3-D Proportional System. Thieme Medical Publisher.
- Tallon-Baudry, & Bertrand. (1999). Oscillatory gamma activity in humans and its role in object representation. *Trends in Cognitive Sciences*, *3*(4), 151–162. https://doi.org/10.1016/S1364-6613(99)01299-1
- Taylor, M. M., & Lederman, S. J. (1975). Tactile roughness of grooved surfaces: A model and the effect of friction. *Perception & Psychophysics*, 17(1), 23–36. https://doi.org/10.3758/BF03203993
- Treisman, A. (1982). Perceptual grouping and attention in visual search for features and for objects. *Journal of Experimental Psychology: Human Perception and Performance*, 8(2), 194–214. https://doi.org/10.1037/0096-1523.8.2.194
- Tsakiris, M., Costantini, M., & Haggard, P. (2008). The role of the right temporoparietal junction in maintaining a coherent sense of one's body. *Neuropsychologia*, 46(12), 3014–3018.
- Tzagarakis, C., Ince, N. F., Leuthold, A. C., & Pellizzer, G. (2010). Beta-Band Activity during Motor Planning Reflects Response Uncertainty. *Journal of Neuroscience*,

- *30*(34), 11270–11277. https://doi.org/10.1523/JNEUROSCI.6026-09.2010
- Ungerleider, L., & Haxby, J. V. (1994). "What" and "where" in the human brain.

 *Current Opinion in Neurobiology, 4(2), 157–165.

 https://doi.org/10.1016/0959-4388(94)90066-3
- Van Aarsen, V., & Overvliet, K. E. (2016). Perceptual grouping by similarity of surface roughness in haptics: the influence of task difficulty. *Experimental Brain Research*, 234(8), 2227–2234. https://doi.org/10.1007/s00221-016-4628-2
- van den Berg, M., Kubovy, M., & Schirillo, J. A. (2011). Grouping by Regularity and the perception of illumination. *Vision Research*, *51*(12), 1360–1371. https://doi.org/10.1016/j.visres.2011.04.013
- van Wijk, B. C. M., Beek, P. J., & Daffertshofer, A. (2012). Differential modulations of ipsilateral and contralateral beta (de)synchronization during unimanual force production. *European Journal of Neuroscience*, *36*(1), 2088–2097. https://doi.org/10.1111/j.1460-9568.2012.08122.x
- Verlaers, K., Wagemans, J., & Overvliet, K. E. (2015). The effect of perceptual grouping on haptic numerosity perception. *Attention, Perception & Psychophysics*, 77(1), 353–367. https://doi.org/10.3758/s13414-014-0770-8
- Verstynen, T. (2004). Ipsilateral Motor Cortex Activity During Unimanual Hand Movements Relates to Task Complexity. *Journal of Neurophysiology*, *93*(3), 1209–1222. https://doi.org/10.1152/jn.00720.2004
- Vezzani, S., Marino, B. F. M., & Giora, E. (2012). An early history of the Gestalt factors of organisation. *Perception*, 41(2), 148–167. https://doi.org/10.1068/p7122
- Vickery, T. J. (2008). Induced perceptual grouping. Psychological Science, 19(7),

- 693-701. https://doi.org/10.1111/j.1467-9280.2008.02144.x
- Volberg, G., Wutz, A., & Greenlee, M. W. (2013). Top-Down Control in Contour Grouping. *PLoS ONE*, 8(1). https://doi.org/10.1371/journal.pone.0054085
- Von Der Heydt, R., Peterhans, E., & Baumgartner, G. (1984). Illusory contours and cortical neuron responses. *Science*, *224*(4654), 1260–1262. https://doi.org/10.1126/science.6539501
- Vukelić, M., Bauer, R., Naros, G., Naros, I., Braun, C., & Gharabaghi, A. (2014).
 Lateralized alpha-band cortical networks regulate volitional modulation of beta-band sensorimotor oscillations. *NeuroImage*, 87, 147–153.
 https://doi.org/10.1016/j.neuroimage.2013.10.003
- Wagemans, J. (1995). Detection of Visual Symmetries. *Spatial Vision*, 9(1), 9–32. https://doi.org/10.1163/156856895X00098
- Wagemans, J. (2016). Perceptual Organization. *Learning & MemoryMethodology): E. J. WagenmakersSeries Ed.) & J. Serences*, 1(2). Retrieved from http://www.gestaltrevision.be/pdfs/bookchapters/Perceptual_Organization.

 pdf
- Wagemans, J., Elder, J. H., Kubovy, M., Palmer, S. E., Peterson, M. A., Singh, M., & von der Heydt, R. (2012). A century of Gestalt psychology in visual perception: I. Perceptual grouping and figure–ground organization. *Psychological Bulletin*, 138(6), 1172–1217. https://doi.org/10.1037/a0029333
- Wagemans, J., Feldman, J., Gepshtein, S., Kimchi, R., Pomerantz, J. R., van der Helm, P. A., & van Leeuwen, C. (2012). A century of Gestalt psychology in visual perception: II. Conceptual and theoretical foundations. *Psychological Bulletin*, 138(6), 1218–1252. https://doi.org/10.1037/a0029334
- Ward, L. M. (1983). On processing dominance: Comment on Pomerantz. Journal of

- Experimental Psychology: General, 112(4), 541–546. https://doi.org/10.1037/0096-3445.112.4.541
- Wertheimer, M. (1910). Über das Denken der Naturvölker. Barth.
- Wertheimer, M. (1923). Laws of Organization in Perceptual Forms.

 Untersuchungen zur Lehre von der Gestalt II, in Psycologische Forschung. In *A source book of Gestalt psychology*.
- West, R., Jakubek, K., Wymbs, N., Perry, M., & Moore, K. (2005). Neural correlates of conflict processing. *Experimental Brain Research*, 167(1), 38–48. https://doi.org/10.1007/s00221-005-2366-y
- Weyl, H. (1989). Symmetry. 1952. Princeton University Press, Princeton, NJ.
- Williams, J. R. (2008). The Declaration of Helsinki and public health. *Bulletin of the World Health Organization*. https://doi.org/10.2471/BLT.08.050955
- WMA General Assembly. World Medical Association Declaration of Helsinki, World Medical Association § (1964).
- Woods, A. T., Moore, A., & Newell, F. N. (2008). Canonical views in haptic object perception. *Perception*, *37*(12), 1867–1878. https://doi.org/10.1068/p6038
- Zangaladze, a, Epstein, C. M., Grafton, S. T., & Sathian, K. (1999). Involvement of visual cortex in tactile discrimination of orientation. *Nature*, *401*(October), 587–590. https://doi.org/10.1038/44139
- Zaretskaya, N., & Bartels, A. (2015). Gestalt perception is associated with reduced parietal beta oscillations. *NeuroImage*, *112*, 61–69. https://doi.org/10.1016/j.neuroimage.2015.02.049
- Zhang, M., Mariola, E., Stilla, R., Stoesz, M., Mao, H., Hu, X., & Sathian, K. (2005).

 Tactile discrimination of grating orientation: fMRI activation patterns. *Human Brain Mapping*, *25*(4), 370–377. https://doi.org/10.1002/hbm.20107

- Zhang, S. (1998). Fourteen homogeneity of variance tests: when and how to use them. *Annual Meeting of the American Educational Research Association*. https://doi.org/ED419696
- Zhou, H., Friedman, H. S., & von der Heydt, R. (2000). Coding of border ownership in monkey visual cortex. *The Journal of Neuroscience*, *20*(17), 6594–6611. https://doi.org/10.1523/JNEUROSCI.2797-12.2013

APPENDIX I- BIOETHICS COMMITTEE APPROVAL

Vicerrectorado de Investigación



D. RICARDO MAIRAL USÓN, PRESIDENTE DEL COMITÉ DE BIOÉTICA DE LA UNIVERSIDAD NACIONAL DE EDUCACIÓN A DISTANCIA

CERTIFICA: Que a la vista de los informes favorables presentados por los miembros del Comité de Bioética, se adopta el siguiente ACUERDO:

"El proyecto titulado: "Agrupamiento perceptivo en modalidad a: correlatos conductuales y neurofisiológicos" cumple todos los requisitos de idoneidad requeridos por este Comité para proyectos que implican investigación con personas".

Y para que conste, se expide el presente certificado que se remite a D. Antonio Prieto como responsable del Proyecto al que se alude en el acuerdo transcrito.

Madrid, 20 de noviembre de 2013

El Presidente del Comité de Bioética

D. Ricardo Mairal Usón Vicerrector de Investigación

APPENDIX II- INFORMED CONSENT



Comité de Bioética

HOJA DE INFORMACIÓN SOBRE EL PROYECTO DE INVESTIGACIÓN Y/O EXPERIMENTACIÓN¹

Título del Proyecto: AGRUPAMIENTO PERCEPTIVO EN MODALIDAD HÁPTICA: CORRELATOS CONDUCTUALES Y NEUROFISIOLÓGICOS.

Autorizado por la UNIVERSIDAD NACIONAL DE EDUCACIÓN A DISTANCIA.

La legislación vigente establece que la participación de toda persona en un proyecto de investigación y/o experimentación requerirá una previa y suficiente información sobre el mismo y la prestación del consentimiento por parte de los sujetos que participen en dicha investigación/experimentación. A tal efecto a continuación, se detallan los objetivos y características del proyecto de investigación arriba referenciado, como requisito previo a la prestación del consentimiento y a su colaboración voluntaria en el mismo:

1) OBJETIVOS²:

Este estudio tiene dos objetivos principales:

- 1. Investigar en profundidad la forma en que percibimos los estímulos en el sentido del tacto, tanto en sus efectos sobre la conducta como en sus correlatos neurofisiológicos (Actividad cerebral).
- 2. Examinar cómo evolucionan durante el envejecimiento los procesos perceptivos en el tacto, junto con su influencia en el funcionamiento de otros procesos cognitivos.

2) DESCRIPCIÓN DEL ESTUDIO:

El estudio consta de una única sesión de entre 2 y 3 horas de duración incluidos los descansos necesarios.

La tarea que va a realizar consistirá en la exploración de elementos de diferentes formas y texturas con los dedos, presentados en un aparato específicamente diseñado para ello. Después de explorar estos elementos con los dedos de su mano, tendrá que indicar algunas de sus características como su textura y su simetría. Al mismo tiempo registraremos su actividad cerebral utilizando un aparato de registro

electroencefalográfico. Para ello, le colocaremos un gorro en la cabeza con los electrodos necesarios para el registro (34), junto con otros seis electrodos localizados tras las orejas (2), en ambas sienes (2) y encima y debajo (2) del ojo izquierdo. La limpieza previa de la piel en los lugares de colocación de los seis electrodos separados del gorro se realiza con productos no agresivos para la piel y se adhieren a la misma mediante tiras de esparadrapo de fácil separación. Una vez colocado el gorro de goma, se añade agua salina sobre los electrodos para mejorar el registro de su actividad neurofisiológica. Se trata de un procedimiento completamente indoloro e inocuo que permite registrar la actividad cerebral y comprobar qué zonas del cerebro están implicadas en la realización de la tarea realizada.

3) POSIBLES BENEFICIOS:

Los resultados de la investigación contribuirán a mejorar el conocimiento de los procesos perceptivos en el tacto, así como el papel de los procesos inflamatorios en el deterioro de estos mismos procesos durante el envejecimiento.

4) POSIBLES INCOMODIDADES Y/O RIESGOS DERIVADOS DEL ESTUDIO: No existen incomodidades o riesgos conocidos.

5) PREGUNTAS E INFORMACIÓN:

Como participante tiene derecho a preguntar y recibir información sobre todos aquellos aspectos que solicite y en todo momento será informado de la evolución del proyecto.

6) PROTECCIÓN DE DATOS3:

Este proyecto requiere la utilización y manejo de datos de carácter personal que, en todo caso, serán tratados conforme a las normas aplicables garantizando la confidencialidad de los mismos.

La participación en este proyecto de investigación es voluntaria y puede retirarse del mismo en cualquier momento.

Y para que conste por escrito a efectos de información de los pacientes a los que se solicita su participación voluntaria en el proyecto antes mencionado, se ha formulado y se entrega la presenta hoja informativa

En	de	de		
		Antonio Prieto Lara		

CONSENTIMIENTO INFORMADO				
D./D ^a				
He leído la hoja de información que se me ha entregado, copia de la cual figura junto a este documento, y la he comprendido en todos sus términos.				
He sido suficientemente informado y he podido hacer preguntas sobre los objetivos y metodología aplicada en el proyecto de investigación AGRUPAMIENTO PERCEPTIVO EN MODALIDAD HÁPTICA: CORRELATOS CONDUCTUALES Y NEUROFISIOLÓGICOS, que ha sido autorizado por la UNIVERSIDAD NACIONAL DE EDUCACIÓN A DISTANCIA y para el que se ha pedido mi colaboración.				
Comprendo que mi participación es voluntaria y que puedo retirarme del estudio, • cuando quiera; • sin tener que dar explicaciones y exponer mis motivos; y • sin ningún tipo de repercusión negativa para mí.				
Por todo lo cual, PRESTO MI CONSENTIMIENTO para participar en el proyecto de investigación antes citado.				
En de de de				
Fdo				

APPENDIX III - HANDEDNESS INVENTORY

EDINBURGH HANDEDNESS INVENTORY

(Oldfield, 1971; Bryden, 1977)

Nombre:		Varón	[]	Mujer	[]
Fecha:	F. nacimiento:		Ed	lad:		_
Estudios/Profesión:	Observacio	nes:				

INSTRUCCIONES: Marque la casilla correspondiente con

- una cruz, si es la mano que utiliza de modo preferente.
- dos cruces, si es la mano que utiliza de modo muy preferente y además le ++ resultaría imposible o muy dificil hacerlo con la otra mano.
- una cruz, en las dos casillas cuando pueda hacerlo tan bien tanto con una mano como con la otra.

¿QUÉ MANO UTILIZA PARA?	DERECHA	IZQUIERDA	Puntos
1. Escribir			1-2-3-4-5
2. Dibujar			1-2-3-4-5
3. Lanzar un objeto			1-2-3-4-5
4. Limpiarse los dientes			1-2-3-4-5
5. Utilizar un cuchillo (sin tenedor)			1-2-3-4-5
6. Cortar con tijeras			1-2-3-4-5
7. Comer con la cuchara			1-2-3-4-5
8. La mano que coloca en la parte superior de la escoba para barrer			1-2-3-4-5
9. Rascar una cerilla			1-2-3-4-5
10. Levantar la tapa de una caja			1-2-3-4-5

Puntos: 5 si ++ sólo en mano izquierda

4 si + sólo en mano izquierda

3 si + en manos izquierda y derecha

2 si + sólo en mano derecha

1 si ++ sólo en mano derecha

Consistentemente zurdo/a: 50 ptos (Máximo) Consistententemente diestro/a: 10 ptos (Mínimo)

303

APPENDIX IV - ELECTRODE LAYOUT

