

rotated rigidly and in opposite sense around the FP during 750 ms, a first translational event (T1) lasting 150 ms affected one of the surfaces while the other continued to rotate. After this, both surfaces rotated in the baseline pattern for 350 ms until a second 150 ms translational event (T2) was presented. The trial ended with an additional 700 ms rotation period. In order to make T1 irrelevant, it always moved to the upward direction and no response to it was required. However, the direction of T2 was always different and randomly selected from 8 possible alternatives.

The experiments took place in a room with dim illumination. Subjects were instructed to maintain fixation and minimize body movement and eyeblinks during recording blocks. The task of the subjects was to discriminate the direction of T2 ignoring the previous T1. A gray or a colored (red or green) FP was used depending on the experiment. In Experiment

1 a gray FP was used, providing to the subjects no information about which surface was going to be affected by T2. Due to the lack of cueing in this experiment, attention had to be divided between both surfaces in order to succeed in T2 discrimination. However in Experiment 2, the FP color tone warned the subjects where T2 was going to occur, on the red or on the green surface. Here, the color of the FP worked as an endogenous cue that enabled selective attention to the surface with the same color than the FP.

Each experiment was performed in separate sessions carried out on different days. Sessions were comprised by two blocks of 335 trials each. The occurrence of T1 on the red or on the green surface was fixed within a block: in one block it occurred on the red surface and the other on the green one. The presentation order of blocks and experiments was counterbalanced across the

subjects. Two types of trials were used: same-surface (where T1 and T2 occurred in the same surface) and different-surface (where T2 occurred in a different surface than T1). Subjects reported the direction of T2 on the numerical-pad of the Computer keyboard. Incorrect responses were signaled by a 500 ms beep on the Computer loudspeaker.

Electrophysiological data acquisition was carried out on a MEDICID 3E system (Neuronic SA). Disk electrodes (Ag/AgCl) were placed in five active derivations (O1, O2, T5, T6, Oz) of the international system 10/20. All active electrodes were referred to linked earlobes. Inter-electrode impedance was always kept below 5 kOhm. Two bipolar derivations were used to record the electro-oculogram (EOG), with one electrode placed just lateral to the external canthi and another 1 cm above the right eye for horizontal and vertical movements respectively. The signals were filtered between 0.05 and 30 Hz (3 dB down). Additionally, a notch filter with a peak at the power line (60 Hz) frequency was used. In each trial, marks corresponding to stimulus events (onset of T1) were co-registered with the amplified and digitized electroencephalogram (EEG) (12-bit resolution), which was sampled at a rate of 250 Hz and stored on magnetic disk for off-line analysis.

The recorded EEG was windowed with a pre-stimulus baseline of 100 msec before T1 onset, and a 900 msec post-stimulus epoch. EEG segments with artifacts or excessive activity in the EOG were rejected. This eliminated about 5 to 25% of all stimulus events, which resulted in individual ERPs based on the average of around 180 events. Grand average ERPs were calculated for all subjects for each site and condition. All data points were corrected (prior to plotting or measurement) by

subtracting the average pre-stimulus amplitude value.

Percent of correct responses were adjusted to compensate for guessing (guessing-level of 0.125). A two-way repeated-measure (rm) ANOVA was carried out with the psychophysical data using CUE (colored vs. gray FP) and TRIAL-TYPE (same- vs. different-surface) as main factors. Since the color of the dots did not produce any significant effect in subsequent analysis, data were collapsed over this factor in the ERP and behavioral data.

The effect of endogenous cueing on the ERP components were tested with rm-ANOVA and a t-test corrected with non-parametric permutation techniques (Blair RC and Kamiski W, 1993; Galan L et al., 1997). For the rm-ANOVA time windows corresponding to the N200 elicited by T1 and T2 were measured. We named these two N200 as N200a (N200 for T1) and N200b (N200 for T2) respectively. In the case of N200a the time window ranged from 170 to 330 ms, in the case of N200b the window ranged from 621 to 792 ms. A one-way rm-ANOVA was performed with TRIAL-TYPE (same- vs. different-surface) as main factor in each experiment. Besides, differences between same- and different-surface trials of both experiments were also explored. A one-way rm-ANOVA with CUE (colored vs. gray FP) as main factor was performed for each type of trial.

Results

Fig. 2 shows the proportion of correct responses for T2 in colored and gray FP experiments, as a function of whether the two events affected the same or different surfaces. As can be observed in the figure, the subjects' performance for T2 was better when they knew in advance which surface was going to be affected. In the colored FP

experiment (solid line in Fig. 2), T2 was discriminated accurately in both same- and different-surface trials. However when the FP was gray (dashed line in Fig. 2), T2 was discriminated accurately only in same-surface trials. There was a deterioration in performance when T2 occurred on a different surface than the one affected by T1.

These effects were tested in rm-ANOVA that showed highly significant effects of CUE ($F(1,8)=39.9$, $p<0.0002$) and TRIAL-TYPE ($F(1,8)=17.1$, $p<0.0003$). The interaction between these factors was also significant ($F(1,8)=5.1$, $p<0.05$). In planned comparison no trial-type effect was found in experiment 2 (colored FP). The presence of the endogenous cue made possible to discriminate T2 regardless it affected the same or a different surface than T1. However when subjects did not have advanced information on the surface which would be affected by T2 (experiment 1), performance for this event was significantly different depending on trial-type, with same- more accurate than different-surface trial ($F(1,8)=11.6$, $p<0.01$).

The generally better scores obtained in experiment 2 compared to experiment 1 were also tested using planned comparisons. This analysis showed significant differences between same- ($F(1,8)=11.7$, $p<0.01$) and different-surface trials ($F(1,8)=20.1$, $p<0.002$) of both experiments.

The grand average ERPs obtained from T5 and T6 derivations are displayed in Fig. 3a. The ERPs for the different conditions, - same- versus different-surface trials-, in experiments 1 and 2 are shown superimposed. Two negative peaks corresponding to the occurrence of T1 and T2 were present in the individual ERPs in all participants. A modulation in the amplitude of N200a depending on FP color was found. As expected the amplitude of N200a was smaller in different- than in same-surface

trials when an endogenous cue informed in advance the subjects on the position of T2.

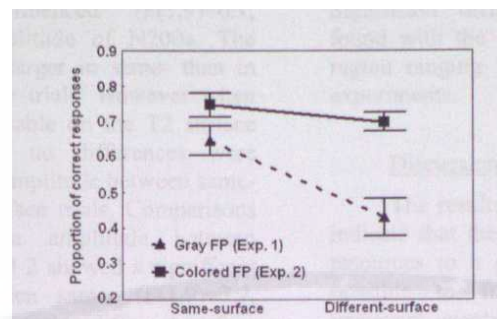


Fig. 2. Means and standard errors of correct responses for T2 as a function of whether the two events affected the same or different surfaces. Each line represents a different experiment. Responses were more accurate in Experiment 2 (colored FP) for both type of trial. However subjects' performance dropped in Experiment 1 (gray FP) in different-surface trial.

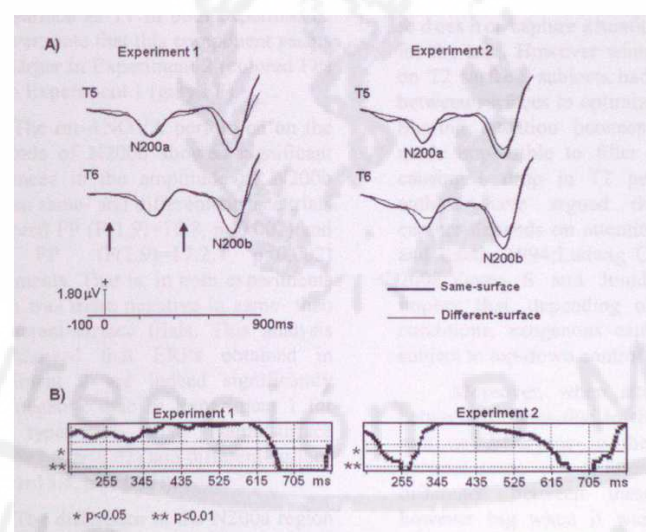


Fig. 3. (A) Grand average ERP from Experiment 1 and 2. Responses to same- and different-surface trials are overlaid. The time axis is referred to the onset of the first event. The two arrows indicate times when events were presented. (B) Observed significant level for the difference between same- and different-surface trials for all time points in both experiments.

The rm-ANOVA showed that the presence of a cue (Experiment 2) significantly influenced ($F(1,9)=6.1$, $p<0.03$) the amplitude of N200a. The component was larger in same- than in difference-surface trials. However when no cue was available on the T2 surface (Experiment 1), no differences were found in N200a amplitude between same- and different-surface trials. Comparisons regarding N200a amplitude between Experiment 1 and 2 showed a significant difference between same- ($F(1,9)=7.7$, $p<0.02$) but not between different-surface trials with a more negative component in same-surface trials of Experiment 2.

As can be observed in Fig. 3a, the negativity provoked by the second translation, the component N200b, was larger in trials where T2 occurred on the same surface as T1 in both experiments. However, note that this component seems to be larger in Experiment 2 (colored FP) than in Experiment 1 (gray FP).

The rm-ANOVA performed on the amplitude of N200b showed significant differences in the amplitude of N200b between same- and different-surface trials in colored FP ($F(1,9)=16.8$, $p<0.002$) and gray FP ($F(1,9)=17.2$, $p<0.002$) experiments. That is, in both experiments N200b was more negative in same- than in different-surface trials. This analysis also showed that ERPs obtained in Experiment 2 are indeed significantly more negative than in Experiment 1 for both types of trial (same-surface ($F(1,9)=7.6$, $p<0.02$) and different-surface ($F(1,9)=13.4$, $p<0.005$)).

The difference in the N200a region (from 210 ms to 290 ms) between neural responses related to the two types of trials was found significant ($p<0.03$) in the t- test corrected with permutation

techniques (Fig. 3b) for Experiment 2 (colored FP) but not for Experiment 1 (gray FP). Significant differences ($p<0.03$) were also found with the same technique in the N200b region ranging from 620 to 792 ms of both experiments.

Discussion

The results obtained in the present study indicate that the prior allocation of attentional resources to a given object by a cue makes possible to filter out uninformative and irrelevant events taking place in other objects, precluding automatic attentional capture. Here, cueing with the color of the FP prevented interference of an irrelevant T1 on the discrimination of subsequent T2 affecting another surface. This result supports and extends Hillstrom and Yantis finding (Hillstrom AP and Yantis S, 1994) that a motion event per se does not capture attention if it is irrelevant for the task. However when no cue was given on T2 surface, subjects had to divide attention between surfaces to optimize its discrimination. Sharing attention between the two surfaces made impossible to filter out the first event causing a drop in T2 performance. Several authors have argued that stimulus-driven capture depends on attentional settings (Bacon and Egeth, 1994; Ludwig CJ and Gilchrist ID, 2002; Yantis S and Jonides J, 1990). This implies that, depending on the experimental conditions, exogenous capture of attention is subject to top-down control.

Moreover, when attention was divided between surfaces due to the lack of cue there was no difference in the N200a amplitude between same- and different-surface trials. The difference between these conditions was however big when it was possible to focus attention in one surface. The reduced N200a (observed in two-surface trials when an endogenous cue was provided) supports the existence of a filtering process for irrelevant

events in early visual areas when attention is previously allocated elsewhere. However the processing of the irrelevant TI that affects the cued surface cannot be prevented and a well defined N200a component is observed in this case, confirming the conclusion stated in the paragraph above.

On the other hand, the fact that the negativity produced by the second event (the N200b component) was larger in same- than in different-surface trials of both experiments could be an evidence of summation of the neural activation produced by the first and the second event in these trials. Moreover, the presence of a larger N200b in same-surface trials after endogenous cueing compared to when this cue was absent, suggest an interaction between stimulus-driven (the occurrence of a previous translation) and goal- directed (the endogenous cue) mechanisms (Corbetta M and Shulman GL, 2002; Pashler H et al, 2001). Actually, some studies have reported increases in the baseline activity of neurons (Kastner S et al., 1999; Luck SJ et al., 1997; Ress D et al., 2000; Shulman GL et al., 1999) during attention tasks and have proposed that it could potentiate an enhancement in stimulus-evoked responses (Ress D et al., 2000). It is possible that the activation caused by the cue in the Experiment 2 plus those produced by the occurrence of the first translational event facilitated the response of the neural population to the second event causing a larger ERP.

However it cannot be rule out that the small reduction observed in the amplitude of N200b in different-surface trials compared to same-surface trials when the cue is available could be also influenced by an exogenous modulation produced by TI that attenuates the endogenous effect on the component. But

if this exogenous attenuation does exist, it is not enough to produce behaviorally a two-object interference. Nevertheless, an experimental design that Controls the possible exogenous driving of TI from of the endogenous effects produced by the cue should be carried out.

Taken together the results obtained in this study suggest that the occurrence of a translational event in one surface is not sufficient to capture automatically attention when it has been endogenously allocated in another surface. The capacity of a motion event for biasing the sensorial processing in favor of one stimulus depends on the pre-established attentional set. It is not the translation per se but its occurrence in the selected object-file what influenced the amplitude of the N200 component in this study. Visual selection is a process that, depending on the context, differentially weighs stimulus-driven and goal- directed influences.

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5.

Discusión general

To see what is in front of one 's nose needs a constant struggle
George Orwell, 1946

Los resultados que se discuten a continuación, aportan evidencias acerca del substrato anatómico de la modulación atencional orientada a objetos inducida con el paradigma de las superficies transparentes. Se demuestra además que la magnitud de la supresión sensorial reflejada en la N200 es un índice de la cantidad de información disponible para la toma de decisión.

Atención orientada a objetos.

Los resultados obtenidos en este trabajo de tesis replicaron resultados anteriores obtenidos por nuestro grupo de trabajo^{167,168} los cuales habían reportado que es más fácil discriminar dos eventos de movimiento sucesivos cuando estos pertenecen a la misma superficie (sección 4.1). Como había sido también referido, la exactitud de la discriminación disminuye cuando ambos eventos están ubicados en superficies diferentes.

Dada la condición de superposición espacial de las superficies, estos datos sólo resultan comprensibles bajo la perspectiva de un modelo orientado a objeto. Este modelo plantea que es más fácil evaluar atributos de un mismo objeto que de dos objetos diferentes^{38,87,174}. La atención visual, propone el modelo, es guiada por la organización de la escena, por lo que la selección de información relevante tiene lugar entre representaciones complejas (objetos) que se derivan de la organización perceptual y que compiten por el control atencional.

Pero las dificultades creadas por la estructuración de la escena con movimiento transparente para realizar dos discriminaciones en objetos diferentes, no son exclusivas para atributos de movimiento. Dificultades similares surgen cuando deben juzgarse simultáneamente combinaciones de atributos de movimiento y forma e incluso, sólo para atributos de forma (sección 4.5). La interferencia que se genera durante el procesamiento de características de más de un objeto, no pudo ser evitada informándole con anticipación a los sujetos la combinación específica de los atributos a discriminar y la superficie de ubicación de los mismos.

El hecho de que no se originara una interferencia entre atributos pertenecientes a la misma superficie pero provenientes de dominios de procesamiento diferentes (como el dominio de forma y el de movimiento) evidencia la existencia de una dependencia o relación

entre los dominios cuando las características o atributos a juzgar pertenecen al objeto atendido. Estudios previos, que habían constatado la presencia de una facilitación en el procesamiento de atributos pertenecientes al mismo objeto perceptual^{7,9,179}, se habían limitado a explorar el fenómeno dentro del mismo módulo o dominio de procesamiento sensorial. La única evidencia experimental previa a la encontrada en este trabajo de la existencia de una relación entre los dominios, para el procesamiento no espacial de atributos, fue la reportada por O'Craven y cols¹³⁰ en un estudio de IRMf. Estos autores demostraron la presencia de activación simultánea en áreas de las vías dorsal y ventral cuando los atributos procesados pertenecían al objeto atendido. Sin embargo, y hasta donde conocemos, los resultados de nuestro trabajo constituyen la primera evidencia psicofísica de una facilitación que se extiende a través de los dominios para el procesamiento de los atributos del objeto atendido.

Este hallazgo apoya la hipótesis de la competencia integrada propuesta por Duncan^{29,35,37,172}, la cual propone que una vez que un objeto gana ventaja en el procesamiento en un subsistema neural (por ejemplo, en el subsistema que analiza la forma o en el que analiza el movimiento), esta ventaja es transmitida al resto de los subsistemas. En el caso de nuestro estudio la hipótesis de Duncan funcionaría de la siguiente manera: el preaviso de atender a los cuadrados (competencia controlada), preactiva selectivamente un grupo de neuronas pertenecientes al subsistema que analiza la forma. Dentro de este subsistema, este grupo de neuronas tendrían ventaja de procesamiento sobre cualquier otro grupo que analice otro tipo de forma (competencia dentro del subsistema). La ventaja de este conjunto es entonces transmitida a las neuronas que procesan la dirección de los cuadrados en el subsistema que analiza el movimiento (integración entre subsistemas). De esta forma la atención actúa como un mecanismo que refuerza el procesamiento simultáneo de atributos de la superficie atendida aún cuando estos sean analizados en dominios tan diferentes como el de forma y movimiento.

Modulación atencional basada en objeto de la actividad eléctrica cerebral: su dependencia de la agudeza perceptual.

La interferencia entre los juicios pertenecientes a dos superficies también se puso de manifiesto en una supresión del componente N200 asociado con el estímulo no atendido (sección 4.1). Como había sido planteado en estudios anteriores^{134,166}, este resultado tampoco es compatible con un modelo de la atención que a manera de reflector selecciona regiones del espacio. Según este modelo, es inevitable seleccionar todos los estímulos ubicados dentro de la región atendida; de lo que se deriva que no es posible que exista supresión de los

componentes tempranos del PE asociado a un estímulo no atendido ubicado muy próximo o en la misma posición que el estímulo relevante^{61,63,109}. Dado el carácter unitario e indivisible del foco de atención^{62,23,184}, este modelo no puede explicar que en nuestros estudios se haya originado una supresión en relación con un estímulo no atendido en la misma región espacial donde se encontraba el atendido.

Sin embargo, un resultado completamente novedoso de este estudio fue el hallazgo de que la amplitud de la N200 depende de la exactitud de los sujetos en el juicio de dirección de la traslación (sección 4.1). Los ensayos donde los sujetos cometieron errores en la evaluación de la segunda traslación (T2), estuvieron asociados con una reducción considerable en la amplitud de este componente. La reducción de la N200 fue mayor cuando T2 ocurrió en la superficie no atendida. Estos resultados pueden ser explicados por medio de la teoría de detección de señales (TDS)⁶⁰, la cual ha sido previamente utilizada para modelar los procesos de decisión durante juicios de la dirección de movimiento dominante en pantallas compuestas por puntos aleatorios en movimiento.

En estos modelos son comparadas las respuestas de distintas neuronas selectivas a la dirección del movimiento visual. Si la actividad de las neuronas selectivas a la dirección dominante (llamada *señal*), es mayor que la actividad de las neuronas selectivas para el resto de las direcciones de movimiento (considerado *ruido*), el resultado es una respuesta correcta. En este caso, la distribución de las respuestas de las neuronas con la actividad considerada señal (de acuerdo con datos obtenidos de registros intracorticales en monos), se desplaza a valores mayores, y solapa parcialmente, la distribución de las respuestas de las neuronas con ruido^{11,15}. Este modelo predice exitosamente la ejecución conductual cuando sus parámetros son ajustados a los datos de las neuronas.

La variación en la amplitud de la N200 en función de la agudeza perceptual puede ser explicada con un cuadro teórico similar. Si asumimos que esta negatividad es una función monótona del nivel de disparo total de las neuronas con señal y con ruido en el área cerebral que analiza el movimiento en el hombre (MT+), este componente puede ser tomado como un índice de la cantidad de información disponible para la toma de decisión. Bajo supuestos razonables acerca de la distribución de la tasa de respuestas de estas neuronas (como que la distribución es normal, con desviación estándar proporcional a la media, y media mayor para la señal que para el ruido), es posible demostrar con simulaciones de Monte Carlo que el valor esperado de la actividad global es menor para ensayos con respuestas incorrectas que para los ensayos con respuestas correctas. El efecto de la atención (condición de misma- vs. distinta- superficie), puede añadirse al modelo como un cambio hacia valores más bajos de la respuesta