Reach trajectories reveal delayed processing of low spatial frequency faces in developmental prosopagnosia

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Developmental prosopagnosia (DP) is characterized by a selective deficit in face recognition despite normal cognitive and neurological functioning. Previous research has established configural processing deficits in DP subjects. Low spatial frequency (LSF) information subserves configural face processing. Using hybrid stimuli, here we examined the evolution of perceptual dynamics and integration of LSF information by DP subjects while they pointed to high spatial frequency (HSF) face targets. Permutation analysis revealed a 230-ms delay in LSF processing by DP subjects as compared to controls. This delayed processing is likely to contribute to the difficulties associated with face recognition in DP subjects and is reflective of their alleged reliance on local rather than global features in face perception. These results suggest that quick and efficient processing of LSF information is critical for the development of normal face perception.

Keywords: Spatial frequency; Developmental prosopagnosia; Face processing; Reach trajectories.

Humans exhibit a preference for faces from the very early stages of life (Johnson & Morton, 1991; Pascalis & de Schonen, 1994), and use faces to extract information about the identity, gender, and emotions, as well as the intentions, of other individuals. Research conducted over the past decades has significantly advanced our understanding of the cognitive and neural processes involved in intact face recognition as well as in related disorders. Developmental prosopagnosia (DP) is a selective deficit in face processing in the context of intact cognitive and neurological functioning. Although it is suggested that the condition is heterogeneous in nature (i.e., individuals with DP show variable patterns of face processing deficits: Duchaine & Nakayama, 2005; Harris, Duchaine, & Nakayama, 2005; Le Grand et al., 2006), a large number of studies have demonstrated a consistent deficit in configural processing of faces (Farah, Wilson, Drain, & Tanaka, 1998; Maurer, Grand, & Mondloch, 2002). To date, the cause of this configural processing deficit is not known.

Early research suggested that low spatial frequency (LSF) information facilitates configural or global processing of stimuli, while high spatial frequency (HSF) information supports feature based processing (Sergent, 1986; Sergent & Hellige, 1986). Some recent studies have focused on the role of LSF in configural processing of faces (Goffaux & Rossion, 2006). Rapid and efficient processing of facial information is thought to be supported by LSF information (Goffaux, Hault, Michel, Vuong, & Rossion, 2005; Goffaux & Rossion, 2006). Recently, we demonstrated the importance of LSF information in face processing, in terms of both early processing of LSF information and LSF-driven rapid categorization of faces (Awasthi, Friedman, & Williams, 2011a, 2011b). Taken together, these results indicate primacy of LSF in face processing.

Deriving a global representation from local components is critical during face perception and DP subjects are reported to be impaired in configural face processing despite extended exposure (Behrmann, Avidan, Marotta, & Kimchi, 2005). Although subjects with

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DP exhibit face processing impairments, their capacity to integrate visual information at various spatial scales, from low to high spatial frequencies, remains untested. This question is particularly acute, given that, in ecological conditions of viewing, spatial frequency bands are naturally integrated to form a coherent percept. We examined whether the abnormal face perception abilities observed in DP subjects could be attributed to abnormal or delayed LSF processing.

We used the experimental paradigm and setup described by Awasthi et al. (2011a) to explore the relative role of LSF information in face processing in DP subjects. Together with DP subjects, age- and sex- matched healthy controls performed a sexcategorization task with hybrid faces. We used reaching trajectories as our dependent measure to examine the evolution of the perceptual dynamics and integration of LSF information in face processing.

Reaching trajectories as a continuous behavioral measure can provide a window on the temporal dynamics of the perceptual decision-making process (Song & Nakayama, 2009; Spivey & Dale, 2004). In reaching, the continuous nature of arm movements allows observation of the state of the decision-making process before a final decision is made on a trial-bytrial basis, as opposed to discrete behavioral measures. Tracking of hand movements is reported to provide unusually high-fidelity, real-time access to fine-grained traces of the perceptual phenomena (Freeman & Ambady, 2011; Freeman, Dale, & Farmer, 2011; Spivey & Dale, 2006). Analyzing the shapes of the trajectories allows early access to the state of the decision-making process while the subjects reach to the targets.

A "change of mind" in everyday decision-making is reflected in the shifts present in arm movements that accompany perceptual decisions (Walsh & Anderson, 2009). In contrast to discrete behavioral measures, such as reaction times and accuracy, visually guided hand reaching can serve as a useful tool to examine the unfolding decision-making process. Hand movements serve as a *continuous* measure as opposed to *discrete* saccades involved in eye tracking (Magnuson, 2005). Reaching trajectories can index rapid shifts in the processing stages and can reveal "hidden" cognitive states that are otherwise not captured by discrete traditional measures (Resulaj, Kiani, Wolpert, & Shadlen, 2009; Song & Nakayama, 2009).

In this study, we were interested in exploring the differences between DP subjects and controls in processing LSF components of faces when the HSF component is the target. In order to observe the subtle differences in processing, which occur before the final decision is made, we needed a continuous measure (as opposed to a discrete one), and reaching trajectories provide an ideal method to examine how the decision evolves. In the present study, subjects start moving before they arrive at a decision and their arm movements allow us to observe how the decision evolves. Consequently, as we forced subjects to move early, reliable reaction time measures cannot be obtained. Other discrete measures do not provide information about partially active alternatives that are reflected in arm movements. Arm movements, however, can index early versus late processing and integration of the two spatial frequency bands being examined here. Through a detailed examination of arm trajectories, we expected to observe differences between controls and DP subjects in early LSF processing, reflected in the congruent and incongruent conditions (outlined in the stimuli-design section).

METHOD

Subjects and screening procedure

Seven subjects with DP as well as seven age- and sexmatched control subjects (DP subjects: two men, mean age: 41.2 years, SD = 17; controls: two men, mean age: 42.3 years, SD = 18) participated in the study. All subjects had normal or corrected-to-normal vision and gave written, informed consent before participation. DP subjects were recruited from the Macquarie Centre for Cognitive Science (MACCS) Prosopagnosia register (www.maccs.mq.edu.au/ research/projects/prosopagnosia/register/), as well as from the local community. They were tested for contrast sensitivity, using the Functional Acuity Contrast Test (FACT) (Vision Sciences Research Corporation, 2002); color blindness, using the Ishihara Test for Color Blindness (Ishihara, 1925); and visual object recognition, using subtests of the Birmingham Object Recognition Battery (BORB) (Riddoch & Humphreys, 1993) and the Raven colored progressive matrices (Raven, Raven, & Court, 1998). The DP subjects were also tested with the Autism Spectrum Quotient (AQ) (Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001). All DP subjects performed within the normal range on the above-mentioned tests. Their face recognition skills were tested with the Cambridge Face Memory Test (CFMT) (Duchaine & Nakayama, 2006b), the Cambridge Face Perception Test (CFPT) (Duchaine, Germine, & Nakayama, 2007a; Duchaine, Yovel, & Nakayama, 2007b), and the MACCS Famous Faces Test (see supplementary information from Palermo, Rivolta, Wilson, & Jeffery (2011) for details of the test; see Appendix 1 for individual results). DP subjects scored 2 SD below Australian norms (Z scores: -0.32 to -2.76, see Appendix 1: also see Bowles et al., 2009, for normative data). All procedures were approved by the Human Research Ethics Committee of Macquarie University.

Apparatus, stimuli, and design

With GIMP (www.gimp.org), unfamiliar face images were converted to grayscale, and external features (neck and hairline) were removed. The images were resized to 400×400 pixel resolutions, and the mean luminance was approximately the same for all pictures. Using Matlab (The Mathworks, Inc., Natick, MA, USA), they were Fourier transformed and multiplied by low-pass and high-pass Gaussian filters to create LSF (below 8 cpf) and HSF (above 25 cpf) versions of each image. These were then superimposed to create the final LSF-HSF hybrid images with the algorithm adapted from Schyns and Oliva (1999). The stimuli were the same as those used in Awasthi et al. (2011a).

Four combinations of hybrid images were used in the experiment. Either male or female was assigned as the target at the beginning of the experiment for each participant (in a counterbalanced fashion) for the entire experiment (e.g., point to the female face). At viewing distance, the HSF face was visible; therefore, it was effectively always the target. A three-factor, withinsubjects design was used, the factors being Target Location (left or right), Target Congruity (congruent, incongruent) and Distractor Conflict (present, absent). All factors were fully crossed, yielding eight experimental conditions. Congruity was defined as the sex of the HSF face of the correct target being the same as that of the LSF face. Thus, MM and FF were congruent whereas FM and MF were incongruent conditions. For instance, in the hybrid image MM, the first letter (M) of the hybrid indicates the sex of the LSF face (Male) and the second letter (M) indicates the sex of the HSF face (M). For hybrid FM, the LSF face is Female and the HSF face is Male (Figure 1).

We also manipulated whether the face on the other side of the target location held a distractor (e.g., an LSF female face) or not (e.g., both the HSF and LSF faces on the non-target side were male). There was no HSF distractor. Two hybrid faces were presented at the leftand right-most sides of the touch screen monitor (Figure 1b). Presentation software (Neurobehavioral Systems, Albany, CA, USA) was used to present the stimuli. The stimuli had a mean width of 5.7° visual angle and were presented 21.7° from fixation.

Procedure

Subjects sat in a quiet, dark room at a table with a LCD touch screen (70×39 cm, 1360×768 pixels, 60 Hz) positioned approximately 70 cm in front of them. Each trial began with subjects placing their right index finger on a centrally located button in front of the touch screen. Hand movements were tracked with an Optotrak Certus Motion Capture System (Northern Digital, Inc., Waterloo, ON, Canada) at a 200-Hz sampling rate. Two small markers—infrared light emitting diodes (LEDs)—were attached to the index fingertip of the right hand. The starting position (a button) was aligned with the body midline, approximately 20 cm in front of the subjects. The tracking system was calibrated at the beginning of each experiment.

Subjects were instructed to maintain fixation on a cross at the center of the screen (that appeared for 1000 ms followed by the hybrid faces), before reaching out and touching the target. Subjects had to begin their reaching response within 350 ms of target onset. The trials were aborted when started too early (before the target onset) or too late (after 350 ms). For all responses, feedback was provided onscreen. In addition to two blocks of training, 10 blocks of 40 trials each were carried out with adequate breaks and the experiment finished within an hour. Only the correct response trials were used for further data analysis. The DP subjects had a mean accuracy rate of 92.5% (SD = 4.6) while controls had a mean accuracy rate of 94.2% (SD = 2.3).

Analysis and statistics

Movement data was analyzed with Matlab. We used cubic splines for data smoothing and interpolation when markers were occluded (for less than 10% of the trajectory). We calculated the maximum deviation from a straight-line path from start to end of the movements. We then defined maximum curvature as the ratio of this deviation to the length of the straight-line path (Atkeson & Hollerbach, 1985; Smit & Van Gisbergen, 1990). The average maximum curvature was computed for all subjects in the eight conditions and used as the dependent variable. Mean trajectories of four conditions for DP subjects and controls, are shown in Figure 2.

A mixed-design ANOVA was carried out with Experiment Group (controls, DP subjects) as a *betweensubjects* factor, and Target Congruity (congruent, incongruent), Distractor Conflict (present, absent), and Target Location (left, right) as *within-subjects* factors. We also

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(a)

(b)



LSF Female- HSF Female (FF)



LSF Male- HSF Female (MF)



LSF Male- HSF Male (MM)



LSF Female- HSF Male (FM)



Figure 1. Face stimulus set and experimental setup used in the experiment. (a) LSF-HSF hybrid images of all four different types. To see the LSF content, the subjects squint, blink, or step back from the figure. (b) Experimental setup showing the touch screen where two hybrid images were presented peripherally. Subjects start each trial at the gray button (s) to reach out and touch the respective black target box on the screen.

compared the curvature across conditions as a function of time (from 100 to 700 ms after target onset). To control for the multiple comparisons that are required in the analysis of continuous data, we used a paired-sample permutation test based on a *t*-statistic (procedure described in detail by Blair & Karniski, 1993).

RESULTS

Between-subjects effects revealed no main effects between the groups, F(1, 12 = 0.153, p = .702. Trajectories were significantly more curved in the incongruent condition as supported by a main effect of Target Congruity, F(1, 12) = 20.1, p < .001, as well as a

significant effect of the LSF distractor as shown by a main effect of Distractor Conflict, F(1, 12) = 74.5, p < .001, and a main effect of Target Location, F(1, 12) = 5.5, p = .03, indicating a biomechanical bias.

For DP subjects, the effect of Target Congruity is smaller than for controls when there is no distractor, but the effect is reversed when the distractor is present (i.e., the congruity effect is larger for DP subjects when the LSF distractor is present). This is shown by a threeway significant interaction between Experimental Group × Target Congruity × Distractor Conflict, F(1, 12) = 4.3, p = .05 (see Figure 3). Post-hoc (Tukey HSD) analysis confirmed a significantly larger curvature due to Target Congruity for controls (mean difference = 0.04, p = .01) than for DP subjects



Figure 2. Mean reaching trajectories for DP subjects (in solid lines) and controls (dotted lines), showing the effect of Target Congruity and Distractor Conflict in pointing to face targets. Trajectories show significantly larger curvature for incongruent targets than congruent target conditions. Further, LSF distractor presence also contributed significantly to larger curvature.



Figure 3. Curvature measures for DP subjects and controls, showing a significant three-way interaction between Experimental Group, Target Congruity, and Distractor Conflict. For DP subjects, the effect of Target Congruity is smaller than for controls when there is no distractor, but the effect is reversed when the distractor is present.

(mean difference = 0.01, p = .07) in no distractor conditions. For LSF distractor-present conditions, however, the congruity differences were significantly larger for DP subjects (mean difference = 0.03, p = .05) than for controls (mean difference = 0.01, p = .09). No other measures or interactions reached significance.

Using permutation analysis, we calculated the curvature difference in congruity conditions between the two experimental groups at each time point from 100 to 600 ms from target onset. The curvature means from each subject were systematically reordered, yielding $2^7 = 128$ permutations for each group (controls and DP subjects). With each permutation, a paired-sample *t*-test was conducted at each time point. We then calculated the maximum *t*-statistic for each permutation, and the difference between conditions was then considered significantly different at the 0.05 level for a given time.

Since, we used a one-sided *t*-test, we take the *t* value that cuts off 0.05% of the tail of the reference distribution. The critical *t* values were 2.8 for controls and 2.9 for DP subjects. For the control group, the effect of congruity was significant (p < .05), beginning at 255 ms, whereas the significant differences in congruity for DP subjects begin at 485 ms after target onset (p < .05) (see Figure 4). This means that, for controls, congruity differences due to LSF processing begin 230 ms earlier than for DP subjects.

GENERAL DISCUSSION

DP subjects are reported to be impaired in configural processing of faces, and, in particular, a failure to integrate visual elements is thought to underlie this



Figure 4. Timing differences in trajectories at the point of significant difference in congruity conditions. For controls, t values start to become significantly different at 255 ms from target onset. For DP subjects, t values start to become significantly different at 485 ms from target onset.

condition (Barton, Press, Keenan, & O'Connor, 2002; Levine & Calvanio, 1989). We examined how DP subjects process LSF-HSF hybrids in contrast to controls. Since the target was in HSF and the accuracy rate for DP subjects was high (and comparable to that of controls), they seem to process HSF information quite well. However, we did observe differences in the processing of LSF information that was apparent from the feature of the trajectories.

The curvature in the reach trajectory is taken as a measure of uncertainty in the decision-making process. The task requires subjects to point to HSF targets, as they do reliably. With facilitation effects of LSF (available in congruent targets), subjects show relatively straighter (less curved) trajectories for congruent targets (both LSF and HSF match the target sex). For incongruent targets, the larger curvature measure suggests uncertainty in reaching to HSF (due to absence of facilitatory LSF information) and reflects asymmetry of spatial frequency integration.

Differences in congruity effects were observed between the groups. The congruity effect for controls is larger when there is no LSF distractor, while, for DP subjects, congruity effects are larger when LSF distractor is present. When there is no LSF distractor, the larger congruity effects for controls (compared to DP subjects) follow from the absence of early facilitatory LSF information (in incongruent targets). When there is a LSF distractor, the facilitatory LSF information is available in the non-target. There is an absence of facilitatory LSF in the incongruent target (LSF-HSF does not match target sex), while at the same time, the facilitatory LSF information in the non-target "pulls" the hand movement toward the non-target. The later use of LSF information, and so a later "pull" toward the non-target, may explain why the congruity effect is larger for DP subjects than for controls in the presence of a LSF distractor.

Examination of the trajectories as a function of time revealed interesting differences between the groups. We observed that trajectory differences for the DP subjects begin much later (i.e., 230 ms later) than for the control group. It seems that DP subjects use LSF information later than controls. This may be due either to slower processing of LSF information or to a deficit in integrating LSF with HSF information. These results confirm that LSF faces interfere with behavioral reaching to HSF face targets (see Awasthi et al., 2011a, 2011b). While this interference was present for DP subjects, it occurred much later than for the control group. This delayed processing is likely to contribute to the difficulties associated with configural face processing.

In this study, we assumed that subjects' arm movements are initially guided by LSF information, and they only later use HSF information to eventually lead them to the target. To further explain this notion, we developed a simple model to qualitatively explain the major findings of this study. Figure 5a shows the average influence of LSF and HSF information as a function of time and fit using the model. Subjects begin gradually using LSF information and later stopped using it (modeled here as a normal probability distribution, in red). With LSF information as a header, subjects also gradually use HSF information, and by the end of the movement, they are solely using HSF information (modeled here as normal cumulative distribution, in blue) and do not use LSF information at all. In the DP experimental group (solid lines), the effect of LSF on the trajectories begins later than in the control group (dashed lines). Based on these average influences of LSF and HSF information, we can predict the trajectories-Figure 5b)-which are qualitatively similar to the mean trajectories for the two groups (Figure 5c). Full details of the model are presented in Appendix 2. Using this simple model, we show that a later use of LSF information for the DP group can explain the differences in trajectories observed in this study.

Similar findings have also been found in prosopagnosia patients with reports of impaired processing of LSF information in facial stimuli (Sergent & Villemure, 1989) and a generalized deficit in global processing (Behrmann et al., 2005). Behrmann et al. (2005) have reported that DP subjects are disproportionately slower in integrating and processing global information, especially at early durations after stimulus onset. In their case, DP subjects tested on the Navon

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Figure 5. (a) These graphs show the average effects of the LSF and HSF components on the trajectory, as a function of time. The LSF component (in red), modeled as a normal probability distribution, has an early effect, but has no effect by the end of the trial. The HSF component (in blue) starts later and by the end of the trial is the sole influence. (b) Predicted trajectories using the model—full details are in Appendix 2. The solid lines are the DP subjects, and the dashed lines are the controls. (c) Mean trajectories, averaged across subjects.

task performed significantly slower than controls for global identification, with further delays observed in asymmetric local-to-global interference. Behrmann et al. (2005) argue further that a failure to perceptually integrate the global-local information appears to be related to the face-processing deficit in DP subjects.

It is also likely that face processing and Navontype global processing depend on different mechanisms. In contrast to the findings by Behrmann et al. (2005), Duchaine et al. (2007b) argue against a simple global processing deficit (obtained through the Navon task) in DP subjects. Examining a significantly larger sample of DP subjects who performed normally in the global-local Navon task, Duchaine et al. (2007b) suggest that the configural processing required by the Navon task is dissociable from face configural processing. Impairment or atypical LSF processing has been reported in other clinical groups that exhibit face-processing deficits, including autism (Deruelle & de Schonen, 1998; Deruelle, Rondan, Salle-Collemiche, Bastard-Rosset, & Da Fonseca, 2008; Deruelle, Rondan, Tardif, & Gepner, 2004; Kätsyri, Saalasti, Tiippana, von Wendt, & Sams, 2008) and children with pervasive developmental disorder (Boeschoten, Kenemans, van Engeland, & Kemner, 2007). All these patients exhibit global processing deficits and show a bias toward the processing of feature-based local information.

Unfamiliar-face recognition relies more on imagebased properties than abstract face-based properties (Burton & Jenkins, 2011), and DP subjects may be relying exclusively on HSF information. LSF information is reported to be sufficient for familiarity judgment, and famous faces can easily be recognized by using coarse-scale blurred information (Sinha, 2002; Sinha, Balas, Ostrovsky, & Russell, 2006). DP subjects typically lose the ability to identify familiar faces, including famous persons, friends, and relatives, or even their own face (Damasio, 1985). It seems likely that an impairment or lack of reliance on LSF information could result in some of the abnormalities observed.

Chatterjee, DeGutis, Mercado, and Nakayama (2011) have reported that DP subjects are likely to have intact configural face processing for gender recognition, but not for identity recognition. In the context of other research reports with mixed findings discussed above, the findings in the current study support the broad hypothesis concerning configural processing deficit, in part attributable to delayed LSF processing. The larger issue has not been fully resolved in favor of configural processing as the underlying basis of DP. However, our findings point to more interesting avenues for further investigation into the nature of DP and face processing.

It has also been reported that human observers are not able to utilize information in all the spatial frequency bands with equal efficiency and rely more on mid-band rather than low or high spatial frequency (Gold, Bennett, & Sekuler, 1999; Kornowski & Petersik, 2003). Through this study, we propose that efficient integration of LSF and HSF bands can enable efficient processing of faces, and a disruption in integrating information from these bands could impair the normal recognition of faces. Recently, Gao and Maurer (2011) reported that 10-year-old children, as well as adults, use LSF information efficiently in facial identity processing. Since DP is a lifelong condition with no associated brain damage, it seems probable that atypical processing of LSF information and subsequent integration failure with higher scales could be a cause of their configural-processing deficit.

The ability of control and DP subjects to process sex categorization and identity information independently is consistent with proposed models of face recognition (for instance, the Bruce and Young model, 1986). Because it is assumed that the magnocellular stream mainly projects to the dorsal pathway (De Yoe & Van Essen, 1988), the findings also lend support to research indicating a specific deficit in the dorsal pathway leading to topographic agnosia, a common co-occurrence with DP subjects (McCarthy, Evans, & Hodges (1996). However, we did not directly test a magno- or parvocellular deficit (and dorsal and/or ventral pathway functioning) in this study. If the hypothesis is verified that a magnocellular system deficiency is at the root of the peculiar visual behavior observed in DP subjects, it would indicate that their different style of processing is present very early in life.

Magnocellular channels are known to provide direct input to the dorsal stream leading to the dorsolateral occipital cortex (Maunsell, 1987) and regions of the posterior parietal lobe (Goodale & Westwood, 2004). Magnocellular channels are known to be more at risk and susceptible to damage (than parvocellular channels) due to disease and other conditions because of their larger structure and axonal thickness (Quigley, Dunkelberger, & Green, 1988). Owing to a much lesser density distribution across the ganglion cell population, damage to magnocellular channels could result in a disruption of visual functions early in the developmental stages. Braddick, Atkinson, and Wattam-Bell (2003) have suggested that the dorsal visual stream is vulnerable during development. Reviewing psychophysical measurements of visual functioning in five developmental disorders, namely, developmental dyslexia, developmental dyspraxia, Williams syndrome, fragile X syndrome, and autism spectrum disorders (ASDs), Grinter, Maybery, and Badcock (2010) argued that the input and functioning of the dorsal visual stream is affected in developmental disorders.

Various studies have reported that newborn humans preferentially process low rather than high spatial frequencies (see de Schonen & Mathivet, 1989, for a review). The delayed processing of LSF information shown by DP subjects here is in agreement with the proposal that some cases of DP might originate in a deficit in the early mechanisms for face processing (de Gelder & Stekelenburg, 2005; Johnson, 2005). Johnson (2005) proposed that face processing is, in part, subcortical and early input is crucial for the normal development of cortical specialized face processing. The current study suggests that fast and efficient processing of LSF information is critical for normal face perception development.

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APPENDIX 1

L-Scores
-3.18
-2.13
-3.49
-2.34
-3.41
-1.39
-2.58

This table shows age, sex and z-scores on Cambridge Face Memory Test (CFMT), Cambridge Face Perception Test (CFPT) and MACCS Famous Faces Test (MFFT).

In italics are the z-scores 2 SD below the mean.

APPENDIX 2

The model sums the effect of LSF information (E_{LSF} , modelled as a normal probability distribution multiplied by a constant):

$$E_{LSF}(t) = M \times \frac{1}{\sqrt{2\pi\sigma_{LSF}}^2} e^{-\frac{(t-\mu_{LSF})^2}{2\sigma^2}}$$

with parameters M, σ_{LSF} and μ_{LSF} , and the HSF information (E_{HSF} , modelled as a cumulative probability distribution):

$$E_{HSF}(t) = \frac{1}{2} \left[1 + \operatorname{erf} \left(\frac{t - \mu_{HSF}}{\sigma_{HSF} \sqrt{2}} \right) \right]$$

with parameters σ_{HSF} and μ_{HSF} , where erf is the error function.

To compute the average amount of information subjects are using at various times in the different conditions, we sum the LSF and HSF components appropriately. If the LSF components are uninformative (i.e., neither target has an LSF target component), we do not include it in the sum. If there exists an LSF distractor, we assume that LSF component acts in a negative way. If there is both an LSF distractor and an LSF component on the target side, we add together the positive and negative components (which sum to zero). In addition, we assume that there is a component of noise, that is a constant proportion of the signal (n), and always positive. We assume that this noise values is the same for both experimental groups. Noise decreases certainty about the target, and so we subtract it from the sum. Finally, we also add a bias, as subjects tend to start moving towards the right. We model the bias *b* as a normal probability distribution:

$$E_{bias}(t) = B \times \frac{1}{\sqrt{2\pi\sigma_{bias}}^2} e^{-\frac{(t-\mu_{bias})^2}{2\sigma^2}}$$

with parameters, B, σ_{bias} and μ_{bias}

We assume that this average amount of information corresponds to the x position (we make this assumption because we are looking at the average, we would not assume that this is true on a trial-by-trial basis). The y position is modelled by a normal cumulative probability distribution (with mean 0.4, SD = 0.2).

We are now able to predict the trajectories for the four conditions. In order to find the seventeen parameters of the model (M, σ_{LSF} , μ_{LSF} , σ_{HSF} , μ_{HSF} , B, σ_{bias} and μ_{bias} for each group, and n), we used the sum of the root mean squared distance between the predictions and the average trajectories (with both resampled to 100 points, with a constant arc length between each point) for the two groups as an error measure. We varied the parameters using nonlinear constrained optimisation in Matlab (*fmincon* function) to minimize the errors. The optimal values were for controls:

$$\begin{split} M &= 0.066, \ \mu_{LSF} = 0.473, \ \sigma_{LSF} = 0.091, \\ \mu_{HSF} &= 0.503, \sigma_{HSF} = 0.089, \ B = 0.026, \mu_{bias} = 0.327, \\ \sigma_{bias} &= 0.089, \text{ and for DPs } M = 0.054, \ \mu_{LSF} = 0.485, \\ \sigma_{LSF} &= 0.096, \ \mu_{HSF} = 0.543, \ \sigma_{HSF} = 0.083, \ B = 0.014, \\ \mu_{bias} &= 0.285, \ \sigma_{bias} = 0.106. \ \text{The noise value (common for both) was } n = 0.218. \end{split}$$

Matlab source code for the model is available by request from the corresponding author.